COMMONWEALTH MYCOLOGICAL INSTITUTE
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The British Mycological Society

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TRANSACTIONS

LONDON
Cambridge University Press
FETTER LANE, E.C.4

CHICAGO
The University of Chicago Press
(Agents for the United States)

BOMBAY · CALCUTTA · MADRAS
Macmillan

TOKYO
Maruzen Company Ltd

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Volume XIX

Edited by

J. Ramsbottom, B. F. Barnes and H. Wormald

CAMBRIDGE
AT THE UNIVERSITY PRESS
1934

PRINTED IN GREAT BRITAIN

S.P.L.

VOL. XIX, PART I Published 25 October 1934

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Price to non-members, Seven Shillings & Sixpence

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TOKYO: MARUZEN COMPANY LTD.

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THE LYNDHURST SPRING FORAY

May 26th–30th, 1933

By E. M. WAKEFIELD

The Spring Foray in 1933 was held at Lyndhurst, in the New Forest, from May 26th to May 30th, with headquarters at the Crown Hotel. After a month of fine, dry weather it seemed unlikely that very many of the larger fungi would be found, and in fact, as will be seen from the list, this foray proved to be the poorest in the records of the Society for fungi of any kind.

Rain fell on the first day of the foray, but this was too late to have any influence on the number of species occurring during the week-end; and as it was continuous and heavy the only result was that it put an early end to collecting on that day.

The first excursion on Saturday, May 27th, was over ground on either side of the road between Lyndhurst and Brockenhurst. In a normal season this should have been good, but very little was obtained, and even the bravest were at last obliged to give up owing to the rain.

On the following day the weather was better, and after a little exploration in the garden of the hotel the party set out in the direction of Lyndhurst Road railway station. In some damp spots at the side of the road various rusts and other microfungi were found, and small copses yielded a few of the larger fungi to increase the list. Monday, May 29th, was spent in the forest region to the west of Lyndhurst, along Highland Water and towards Mark Ash. The ground here was so barren, however, that after lunch a few of the party went by car to Ringwood, and explored the riverside there. The species found in the neighbourhood of Ringwood are indicated separately in the following list, but the other localities visited were all so close to Lyndhurst that they are treated as one.

In the evening on Saturday, May 27th, Dr R. Butcher gave an interesting talk on "Polysaprobic organisms and their value as indicators of the condition of waters." The paper was illustrated by photographs showing typical examples of growths found in polluted waters.

A business meeting was held on the Sunday evening to elect new members and to choose the locality for the Spring Foray in 1934. Considerable discussion on the latter subject led to no definite decision, but the Secretary was asked to make enquiries about Woodhall Spa and Sherwood Forest; the final decision was left to the Council.

It has since been ascertained that the former place is not very promising, and further, a definite invitation has been received from Mr E. M. Day to visit Stroud. It has been decided therefore to hold the 1934 Spring Foray at Stroud, in Gloucestershire.

Complete List of Species gathered during the Foray

HYMENOMYCETES

Russula cyanoxantha (Schaeff.) Fr.
Collybia leucomyosotis Cooke & Smith
Marasmius dryophilus (Bull.) Karst., oreades (Bolt.) Fr.
Panus stypticus (Bull.) Fr.
Nolanea proletaria Fr.
Pholiota adiposa Fr.
Bolbitius titubans (Bull.) Fr.
Inocybe lacera Fr., *near Beaulieu*
Stropharia semiglobata (Batsch) Fr.
Polyporus betulinus (Bull.) Fr., adustus (Willd.) Fr.
Fomes ferruginosus (Schrad.) Mass.
Ganoderma applanatum (Pers.) Pat., laccatum (Kalchbr.) Rea
Polystictus versicolor (Linn.) Fr.
Trametes gibbosa (Pers.) Fr.
Daedalea quercina (Linn.) Fr.
Merulius lacrymans (Wulf.) Fr.
Irpex obliquus (Schrad.) Fr.
Acia fuscoatra (Fr.) Pat.
Odontia papillosa (Fr.) Bres.
Grandinia farinacea (Pers.) Bourd. & Galz.
Stereum hirsutum (Willd.) Fr., spadiceum (Pers.) Fr.
Hymenochaete corrugata (Fr.) Lév.
Corticium praetermissum (Karst.) Bres., porosum B. & C., roseocremeum Bres.
Peniophora hydnoides Cooke & Mass.
Exidia Thuretiana (Lév.) Fr., nucleata (Schw.) Rea
Dacryomyces deliquescens (Bull.) Duby

UREDINALES

Puccinia Anemones Pers., Violae (Schum.) DC., Circaeae Pers., expansa Link, Taraxaci Plowr., Hypochaeridis Oud., Veronicae Schroet., coronata Corda (aecidium on *Rhamnus Frangula*), Caricis (Schum.) Rebent. (aecidium on *Urtica*), Phragmitis (Schum.) Koern. (on *Phragmites* and aecidium on *Rumex*), *Ringwood*
Phragmidium mucronatum (Pers.) Schlecht.
Kuehneola albida (Kuehn.) Magn.
Coleosporium Melampyri (Rebent.) Kleb.
Melampsorella Symphyti (DC.) Bubák, *Ringwood*

USTILAGINALES

Urocystis Anemones (Pers.) Wint.
Entyloma microsporum (Ung.) Schroet.

PYRENOMYCETES

Sphaerotheca pannosa (Wallr.) Lév.
Podosphaera Oxyacanthae (DC.) de Bary
Epichloe typhina (Pers.) Tul.

Lasiosphaeria hirsuta (Fr.) Ces. & de Not., on *Fagus*
Rosellinia velutina Fuck.
Melanomma pulvis-pyrius (Pers.) Fuck., on *Fagus*, fuscidulum Sacc.
Ceratostomella (? vestita Sacc.) on *Fagus*
Calyculosphaeria tristis (Fuck.) Fitzp., on *Fagus*
Stigmatea Robertiani Fr.
Mycosphaerella maculiformis (Fr.) Schroet.
Venturia Rumicis (Desm.) Wint., inaequalis Aderh.
Diaporthe eres Nits. on *Ilex*, leiphaemia (Fr.) Sacc. on *Quercus*
Eutypa spinosa (Pers.) Tul. on *Fagus*, Acharii Tul. on *Fagus* and *Hedera*
Melogramma spiniferum (Wallr.) de Not. on *Fagus*
Diatrypella quercina (Pers.) Fr.
Diatrype Stigma (Hoffm.) de Not.
Hypoxylon semiimmersum Nits. on *Quercus*, serpens (Pers.) Fr. on *Fagus*, cohaerens (Pers.) Fr. on *Fagus*, fuscum (Pers.) Fr. on *Corylus*, rutilum Tul. on *Fagus*, coccineum Bull. on *Fagus*
Ustulina vulgaris Tul. on *Fagus*
Xylaria Hypoxylon (Linn.) Grev.

HYSTERIALES

Hysterium angustatum A. & S. on *Fagus*
Gloniopsis curvata A. & S. on *Fagus*

DISCOMYCETES

Aleuria umbrina Boud.
Ciliaria scutellata (Linn.) Quél.
Taphrina deformans (Berk.) Tul. on Almond, Tosquinetii (West.) Magn. on *Alnus*, Potentillae (Earl.) Johans. on *Potentilla Tormentilla*
Bulgaria inquinans (Pers.) Fr.
Chlorosplenium aeruginosum (Oeder.) de Not.
Dasyscypha virginea (Batsch) Fuck.
Arachnopeziza aurelia (Pers.) Fuck., *Beaulieu*
Mollisia cinerea (Batsch) Karst.
Stegia Ilicis Fr.
Colpoma quercinum (Pers.) Wallr.
Rhytisma acerinum (Pers.) Fr.

PHYCOMYCETES

Synchytrium Taraxaci de Bary & Wor.
Plasmopara nivea Schroet. on *Aegopodium*
Bremia Lactucae Regel on *Lampsana* and *Leontodon*
Peronospora calotheca de Bary on *Galium Aparine*, Myosotidis de Bary on *Myosotis*

DEUTEROMYCETES

Phyllosticta hedericola Dur. & Mont.
Actinonema Rosae (Lib.) Fr.
Oidium alphitoides Griff. & Maubl.
Botrytis cinerea Pers. on *Cheiranthus Allionii*
Trichoderma viride Fr.
Ramularia Primulae Thuem.
Isaria farinosa (Dicks.) Fr.

THE NEWCASTLE FORAY

September 18th–23rd, 1933

By E. M. WAKEFIELD

The thirty-seventh Autumn Foray and Annual General Meeting was held at Newcastle-on-Tyne during the week September 18th–23rd. By kind permission of Prof. J. W. Heslop Harrison and the Council of the College, headquarters were in the Department of Botany of Armstrong College. Here books and microscopes were available, and ample space for work and for the exhibition of specimens.

The attendance was smaller than is usual at autumn meetings, no doubt owing to the certainty that after the long, dry summer there would be very few fungi to be found. About twenty members and friends assembled on the Friday evening, and were received by Prof. and Mrs Harrison in the Department of Botany.

On the Tuesday morning, September 19th, an early start was made by train for Alnwick, where Hulne Park was explored. The ground here was fairly damp in places, and the number of fungi found, though very unlike a normal season's haul, was quite cheering to those who came expecting nothing. Almost at once the debris beneath a large beech yielded numerous specimens of *Xylaria carpophila* in good condition. *Lepiota Bucknallii*, *Tricholoma acerbum*, *Hebeloma subsaponaceum*, *Cortinarius triumphans*, *Pholiota flammans*, and *Pustularia cupularis* were perhaps the most noteworthy finds among the larger fungi. It was interesting to find again *Naumovia abundans* on *Prunella*, which had been seen in 1931 at Belfast. This fungus was found again on the following day at Gibside, so that it is probably not uncommon in the district. *Corticium coronatum*, a new record for Britain, was identified subsequently.

Unfortunately for us, the much-needed rain arrived in the north on the next day, and at first collecting was considerably hampered by heavy showers. Gibside Park, near Rowlands Gill, Co. Durham, was the place selected, and proved interesting ground, which in a normal season would no doubt be rich in fungi. Actually, however, the bag on this day was far less than at Alnwick. The *Naumovia* already mentioned and *Tulasnella violea* were the only specially noteworthy finds.

In the evening, at 8.30 p.m., the President, Prof. W. Brown, delivered his Presidential Address, entitled "The Mechanism of Disease Resistance in Plants."

On Thursday, September 21st, Dipton Woods near Corbridge were explored. At first a pine wood, with numerous stumps and old fallen

trunks, provided work for those interested in the lower Basidiomycetes. A traverse through some open moorland brought the party to a dense mixed wood with a fair amount of undergrowth. This was, however, not very productive of fungi, and very little of any note was secured.

On the next day, at Chopwell Wood, the ground was even more dry and yielded nothing but a few common species of fungi.

In the evening of Thursday, September 21st, Mr J. Ramsbottom had been invited to deliver a popular lecture at the Hancock Museum. The lecture was on "Edible and Poisonous Fungi" and was well attended. By courtesy of the Council of the Natural History Society of Northumberland the Hancock Museum, one of the oldest in the country, was open free to members of the Society during the week.

The Annual General Meeting was held on Tuesday evening, September 19th, when the Officers and Council for the ensuing year were elected as follows: President, Dr B. Barnes; Vice-Presidents, Prof. W. Brown and Mr Carleton Rea; members of Council to replace three members retiring under the Rules, Mr Cartwright, Mr Bartlett, and Mr Carrothers. The Editors and other Officers remain as before. Mrs Alcock was nominated as delegate to the British Association in 1934.

A cordial invitation from the Norfolk and Norwich Naturalists Society and the Council of the Norwich Museum led to the selection of Norwich as headquarters for the Autumn Foray in 1934. The date was left to the Council to decide in consultation with the Norwich members of the Society.

At the close of the meeting, cordial votes of thanks were passed to the various landowners who had permitted visits to their estates. Special thanks were accorded to the Council of Armstrong College and Prof. Heslop Harrison for hospitality, and particularly to Mr A. W. Bartlett for the trouble taken by him in organising the meeting.

For assistance in compiling the attached list of fungi collected the Secretary is especially indebted to Mr Ramsbottom, Mr Pearson, Mr E. W. Mason, and Mr T. Petch.

Complete List of Species gathered during the Foray

A. = Hulne Park, Alnwick; *G.* = Gibside Park; *D.* = Dipton Woods; *C.* = Chopwell Wood.

HYMENOMYCETES

Amanita mappa (Batsch) Fr., *D.*, *C.*, muscaria (Linn.) Fr., *A.*, *D.*, rubescens (Pers.) Fr., *G.*

Amanitopsis vaginata (Bull.) Roze, *A.*, *C.*, fulva (Schaeff.) W. G. Sm., *A.*

Armillaria mellea (Vahl) Fr., *A.*, *G.*, *C.*, mucida (Schrad.) Fr., *A.*

Lepiota cristata (A. & S.) Fr., *A.*, amianthina (Scop.) Fr., *A.*, sistrata Fr., *A.*, Bucknallii B. & Br., *A.*

Tricholoma rutilans (Schaeff.) Fr., *A.*, *G.*, *C.*, saponaceum Fr., *A.*, acerbum (Bull.) Fr., *A.*

Clitocybe aurantiaca (Wulf.) Studer, *A.*, *D.*, *C.*, and var. albida (Gill.) Rea, *D.*, cerussata Fr., *G.*, infundibuliformis (Schaeff.) Fr., *G.*, flaccida (Sow.) Fr., *A.*

Laccaria laccata (Scop.) B. & Br., *A.*

Collybia radicata (Relh.) Berk., *A.*, platyphylla (Pers.) Fr., *G.*, fumosa (Pers.) Quél., *G.*, maculata (A. & S.) Fr., *A.*, *D.*, *C.*, tuberosa (Bull.) Fr., *A.*

Mycena pura (Pers.) Fr., *D.*, *C.*, galericulata (Scop.) Fr., *A.*, *C.*, ammoniaca Fr., *A.*, haematopus (Pers.) Fr., *A.*, *G.*, sanguinolenta (A. & S.) Fr., *A.*, galopus (Pers.) Fr., *A.*, rorida Fr., *A.*

Russula chloroides (Krombh.) Bres., *A.*, nigricans (Bull.) Fr., *A.*, adusta (Pers.) Fr., *A.*, lepida Fr., *A.*, cyanoxantha (Schaeff.) Fr., *A.*, *G.*, *D.*, *C.*, foetens (Pers.) Fr., *A.*, ochroleuca (Pers.) Fr., *A.*, *G.*, *C.*, fellea Fr., *A.*, drimeia Cooke var. Queletii (Fr.) Bat., *A.*, *D.*, fragilis (Pers.) Fr., *A.*, *G.*, and var. fallax (Schaeff.) Mass., *D.*, *C.*, emetica (Schaeff.) Fr., *A.*, atropurpurea (Krombh.) Maire, *G.*, xerampelina (Schaeff.) Fr., *A.*, puellaris Fr., *A.*, vesca Fr., *G.*

Lactarius torminosus (Schaeff.) Fr., *A.*, turpis (Weinm.) Fr., *D.*, blennius Fr., *A.*, uvidus Fr., *A.*, pyrogalus (Bull.) Fr., *A.*, chrysorheus Fr., *A.*, vellereus Fr., *A.*, deliciosus (Linn.) Fr., *A.*, quietus Fr., *A.*, *D.*, rufus (Scop.) Fr., *D.*, glyciosmus Fr., *A.*, serifluus (DC.) Fr., *A.*, mitissimus Fr., *A.*, subdulcis (Pers). Fr., *A.*

Pleurotus sapidus Schulz., *G.*

Cantharellus cibarius Fr., *D.*

Marasmius peronatus (Bolt.) Fr., *G.*, *C.*, esculentus (Wulf.) Karst., *A.*, *D.*, hariolorum (DC.) Quél., *A.*, *G.*, *C.*, impudicus Fr., *D.*, dryophilus (Bull.) Karst., *A.*, *D.*, ramealis (Bull.) Fr., *D.*, *C.*

Androsaceus androsaceus (Linn.) Pat., *D.*

Lentinus cochleatus (Pers.) Fr., *A.*

Pluteus cervinus (Schaeff.) Fr., *G.*, salicinus (Pers.) Fr., *G.*

Entoloma nidorosum Fr., *A.*

Nolanea cetrata (Fr.) Schroet., *A.*, *D.*

Clitopilus prunulus (Scop.) Fr., *A.*

Paxillus involutus (Batsch) Fr., *A.*, *D.*

Pholiota squarrosa (Mull.) Fr., *A.*, spectabilis Fr., *A.*, *D.*, flammans Fr., *A.*, mutabilis (Schaeff.) Fr., *A.*, *G.*

Inocybe geophylla (Sow.) Fr., *A.*, and var. lilacina Fr., *A.*, obscura (Pers.) Fr., *A.*, perlata Cooke, *A.*

Astrosporina calospora (Quél.) Rea, *A.*

Hebeloma crustuliniforme (Bull.) Fr., *A.*, subsaponaceum Karst., *A.*

Galera hypnorum (Schrank) Fr., *A.*, tenera (Schaeff.) Fr., *A.*

Naucoria escharoides Fr., *A.*

Flammula sapinea Fr., *D.*, ochrochlora Fr., *D.*

Cortinarius (Phlegmacium) triumphans Fr., *A.*, (Myxacium) elatior Fr., *G.*, *C.*, (Telamonia) rigidus (Scop.) Fr., *A.*, *G.*, (Hydrocybe) leucopus (Bull.) Fr., *A.*, acutus (Pers.) Fr., *A.*

Crepidotus mollis (Schaeff.) Fr., *A.*

Psalliota sylvatica (Schaeff.) Fr., *A.*

Stropharia aeruginosa (Curt.) Fr., *A.*

Hypholoma sublateritium (Schaeff.) Fr., *A.*, *C.*, fasciculare (Huds.) Fr., *A.*, *D.*, *C.*, hydrophilum (Bull.) Fr., *D.*

Psilocybe uda (Pers.) Fr., *D.*, semilanceata Fr., *G.*, *C.*

Psathyrella disseminata (Pers.) Fr., *A.*, atomata Fr., *D.*

Anellaria separata (Linn.) Karst., *G.*

Coprinus comatus (Fl. Dan.) Fr., *A.*, atramentarius (Bull.) Fr., *A.*, *G.*, micaceus (Bull.) Fr., *A.*, lagopus Fr., *A.*

Boletus luteus (Linn.) Fr., *D.*, elegans (Schum.) Fr., *A.*, viscidus (Linn.) Fr., *A.*, granulatus (Linn.) Fr., *A.*, badius Fr., *A.*, *D.*, variegatus (Sow.) Fr., *D.*, chrysenteron (Bull.) Fr., *A.*, *G.*, subtomentosus (Linn.) Fr., *D.*, *C.*, pruinatus Fr., *A.*, edulis (Bull.) Fr., *A.*, scaber (Bull.) Fr., *A.*

Polyporus nummularius (Bull.) Quél., squamosus (Huds.) Fr., *A.*, *G.*, sulphureus (Bull.) Fr., *A.*, *G.*, giganteus (Pers.) Fr., *A.*, *G.*, betulinus (Bull.) Fr., *A.*, *G.*, *D.*, *C.*, adiposus B. & Br., *G.*, caesius (Schrad.) Fr., *A.*, trabeus Fr., *A.*
Fomes annosus Fr., *A.*
Ganoderma applanatum (Pers.) Pat., *A.*
Poria sanguinolenta (A. & S.) Fr., *A.*, hymenocystis B. & Br., *A.*, *D.*
Polystictus versicolor (Linn.) Fr., *A.*, *G.*, abietinus (Dicks.) Fr., *D.*
Irpex obliquus (Schrad.) Fr., *D.*
Fistulina hepatica (Huds.) Fr., *A.*
Hydnum repandum (Linn.) Fr., *A.*
Grandinia farinacea (Pers.) Bourd. & Galz., *A.*, *G.*, granulosa Fr., *A.*
Hypochnus fuscus (Pers.) Fr., *A.*, fumosus Fr., *D.*, phylacteris (Bull.) Rea, *A.*
Stereum spadiceum Fr., *A.*, *G.*, *D.*, rugosum Fr., *A.*, *G.*, hirsutum (Willd.) Fr., *A.*, *G.*
Corticium Sambuci (Pers.) Fr., trigonospermum Bres., *A.*, coronatum (Schroet.) v. Hoehn. & Litsch., *A.*, botryosum Bres., *A.*, subcoronatum v. Hoehn. & Litsch., *A.*, confine Bourd. & Galz., *G.*, porosum B. & C., *A.*
Corticium polygonium (Pers.) Fr., *C.*, praetermissum (Karst.) Bres., *A.*, albostramineum (Bres.) Bourd. & Galz., *A.*
Peniophora byssoidea (Pers.) v. Hoehn. & Litsch., *A.*, *G.*, velutina (DC.) Cooke, *A.*, setigera (Fr.) Bres., *A.*, hydnoides Cooke & Mass., *A.*, quercina (Pers.) Cooke, *G.*, *C.*
Clavaria cristata (Holmsk.) Fr., *A.*
Platygloea effusa Schroet., *A.*
Exidia glandulosa (Bull.) Fr., *D.*
Tulasnella violea (Quél.) Bourd. & Galz., *G.*
Dacryomyces deliquescens (Bull.) Duby, *G.*, *D.*, *C.*
Calocera viscosa (Pers.) Fr., *D.*, cornea (Batsch) Fr., *G.*

GASTEROMYCETES

Phallus impudicus (Linn.) Pers., *G.*
Lycoperdon giganteum (Batsch) Pers., *A.*, pyriforme (Schaeff.) Pers., *A.*, *G.*
Scleroderma aurantium Pers., *A.*, verrucosum (Vaill.) Pers., *A.*

UREDINALES

Uromyces Alchemillae (Pers.) Lév., *A.*
Puccinia Violae (Schum.) DC., *A.*, *G.*, aegra Grove, *A.*, Lychnidearum Link, *A.*, pulverulenta Grev., *A.*, Epilobii DC., *C.*, Chrysosplenii Grev., *G.*, Chaerophylli Purt. on *Myrrhis odorata*, *G.*, obtegens (Link) Tul., *A.*, Crepidis Schroet., *C.*, Hieracii (Schum.) Mart., *C.*, Chondrillae Corda on *Lactuca muralis*, *C.*, Senecionis Lib., *A.*, Primulae (DC.) Duby, *A.*, Veronicae Schroet. on *Veronica montana*, *A.*, Glechomatis DC., *A.*, Menthae Pers., *A.*, annularis (Str.) Schlecht., *A.*, Acetosae (Schum.) Koern., *A.*, Buxi DC., *A.*, obscura Schroet., *A.*, *D.*, Poarum Niels. (Aecidium on *Tussilago*), *A.*, *C.*, mirabilissima Peck, *A.*
Triphragmium Ulmariae (Schum.) Link, *A.*
Phragmidium mucronatum Schlecht., *A.*, violaceum (Schultz) Wint., *A.*
Coleosporium Tussilaginis (Pers.) Kleb., *A.*
Pucciniastrum Circaeae (Schum.) Schroet., *A.*, *G.*, Epilobii (Pers.) Otth, *A.*
Milesina Blechni Syd., *D.*
Melampsoridium betulinum (Pers.) Kleb., *A.*, *D.*, *C.*

USTILAGINALES

Ustilago violacea (Pers.) Wint., *A.*
Entyloma Calendulae (Oud.) de Bary, *A.*
Urocystis Anemones (Pers.) Schroet. on *Ranunculus repens*, *A.*, *G.*

PLECTASCALES

Elaphomyces granulatus Fr., *D.*
Ctenomyces serratus Eidam, *A.*

PYRENOMYCETES

Sphaerotheca pannosa (Wallr.) Lév., *A.*
Podosphaera Oxyacanthae (DC.) de Bary, on *Vaccinium Myrtillus*, *D.*
Erysiphe Polygoni DC. on *Hypericum*, *A.*, cichoriacearum DC. on *Senecio*, *A.*
Uncinula Aceris (DC.) Sacc., *A.*
Nectria cinnabarina (Tode) Fr., *G.*, *C.*
Claviceps purpurea (Fr.) Tul., *G.*, microcephala (Wallr.) Tul., *D.*
Stigmatea Robertiani Fr., *G.*
Naumovia abundans Dobr. on *Prunella*, *A.*, *G.*
Bertia moriformis (Tode) de Not., *A.*
Sphaerulina Taxi (Cooke) Mass., *A.*
Diatrypella quercina (Pers.) Nits., *A.*
Diatrype Stigma (Hoffm.) Fr., *A.*, disciformis (Hoffm.) Fr., *G.*
Ustulina vulgaris Tul., *A.*
Xylaria Hypoxylon (Linn.) Grev., *A.*, polymorpha (Pers.) Grev., *A.*, carpophila (Pers.) Fr., *A.*
Phyllachora graminis (Pers.) Fuck., *A.*, *C.*
Endodothella Junci (Fr.) Theiss. & Syd., *D.*
Dothidella betulina (Fr.) Sacc., *A.*

HYSTERIALES

Lophodermium Pinastri Chev., *D.*

DISCOMYCETES

Galactinia badia (Pers.) Boud., *D.*
Pustularia cupularis (Linn.) Fuck., *A.*
Lachnea hemisphaerica (Wigg.) Gill., *A.*
Taphrina Tosquinetii (West.) P. Magn., *A.*
Helotium fructigenum (Bull.) Fuck., *A.*
Orbilia xanthostigma Fr., *A.*
Sclerotinia Curreyana (Berk.) Karst., *A.*
Dasyscypha virginea (Batsch) Fuck., *G.*
Trichoscypha calycina (Schum.) Boud., *D.*, *C.*
Mollisia cinerea (Batsch) Karst., *A.*
Fabraea Ranunculi (Fr.) Karst., *A.*
Stegia Ilicis Fr., *A.*, *G.*
Rhytisma acerinum (Pers.) Fr., *A.*, *G.*, *C.*

PHYCOMYCETES

Syzygites megalocarpus Ehrenb. on *Lycoperdon giganteum*, *A.*
Plasmopara nivea Schroet., *G.*
Entomophthora aphrophorae Rostr. on froghoppers, *D.*

DEUTEROMYCETES

Actinonema Rosae (Lib.) Fr., *A.*
Oidium alphitoides Griff. & Maubl., *D.*, *C.*
Botrytis cinerea Pers. on *Scilla*, *A.*
Rhinotrichum repens Preuss, *A.*, Thwaitesii B. & Br., *A.*
Sepedonium chrysospermum (Bull.) Fr., *D.*
Cephalosporium muscarium Petch, on fly, *C.*

Ovularia obliqua (Cooke) Oud., *A.*, *G.*, *C.*, primulana Karst., *A.*
Ramularia Primulae Thuem., *A.*, calcea (Desm.) Ces., *A.*, sambucina Sacc., *A.*, Ajugae Niessl., *A.*, acris Lindr., *A.*, Urticae Ces., *A.*, Taraxaci Karst., *A.*, Cirsii Allesch., *A.*
Fusicladium depressum (B. & Br.) Sacc., *C.*
Cladosporium herbarum (Pers.) Link, on dead flies, *C.*
Cercospora Mercurialis Pass., *A.*, *C.*
Sporocybe Azaleae Peck, *A.*
Stilbella erythrocephala (Ditm.) Lindau, *A.*
Isaria farinosa (Holmsk.) Fr., *C.*, sphecophila Ditm. on an ichneumon, *C.*
Hymenostilbe arachnophila (Ditm.) Petch, on spiders, *D.*, *C.*

MYCETOZOA FOUND DURING THE FORAY OF THE BRITISH MYCOLOGICAL SOCIETY AT NEWCASTLE, SEPTEMBER 18TH–21ST, 1933

By G. LISTER

After the drought of the summer months it was not surprising that our harvest of Mycetozoa was not large. The total list of species found was twenty-two, one of which, however, *Cribraria macrocarpa*, had not been recorded before from England, and only twice from Scotland. On September 19th the Hulne Abbey Woods were visited, where fine groves of ash, sycamore, oak and Douglas Spruce clothed the steep banks of a stream; eleven species of Mycetozoa were found. On September 20th, Gibside Park should have given very good hunting, but heavy rain proved impeding. On September 21st we were conveyed to Dipton Moor, where the woods of Scotch Fir, with undisturbed fallen branches, provided many colonies of species usually associated with coniferous wood. It was here that *Cribraria macrocarpa* was found on dead branches, in a rather mouldy condition; *C. rufa* was abundant. Yellow plasmodium, creeping in a thick bed of pine-needles, was brought away and kept moist; after five weeks it developed typical sporangia of *Leocarpus fragilis*.

In the following list *H.*, *G.* and *D.* refer to gatherings from Hulne Abbey Woods, Gibside and Dipton Woods respectively.

Ceratiomyxa fruticulosa (Mueller) Macbr., *D.*
Physarum nutans Pers. and var. leucophaeum Lister, *H.*
Fuligo septica (L.) Gmel., *H.*
Leocarpus fragilis (Dicks.) Rost., *D.*
Didymium difforme (Pers.) Duby, *H.*
Stemonitis fusca Roth, *H.*
S. flavogenita Jahn, *H.*
Comatricha nigra (Pers.) Schroeter, and var. alta Lister, *D.*
C. typhoides (Bull.) Rost., *H.*
Cribraria argillacea Pers., *G.*
C. rufa (Roth.) Rost., *D.*
C. macrocarpa Schrader, *D.*
Dictydium cancellatum (Batsch) Macbr. var. fuscum, *D.*
Tubifera ferruginosa Gmel., *D.*
Lycogala epidendrum (L.) Fries, *D.*
Trichia verrucosa Berk., *D.*
T. affinis de Bary, *H.*
T. decipiens (Pers.) Macbr., *H.*
T. Botrytis Pers., *G.*, *D.*
Arcyria cinerea (Bull.) Pers., *H.*, *G.*, *D.*
A. denudata (L.) Wettst., *H.*
A. incarnata Pers., *H.*

PRESIDENTIAL ADDRESS

By W. BROWN, M.A., D.Sc.

MECHANISM OF DISEASE RESISTANCE IN PLANTS

The subject of disease resistance in plants, considered from the point of view either of academic or practical interest, is of too wide a scope to allow of adequate treatment in such an address as I propose to give. Relevant material could probably be culled from almost any paper dealing with a plant pathological subject. There is the variation of susceptibility from one plant or variety to another and the different behaviour of the same plant under different environmental conditions. Viewed from another standpoint, there are such matters of interest as the pathogenic range of various fungal parasites and the differences in virulence shown by strains, biological races, etc., of the same fungal species. Data of this type would all contribute to make up the full story of disease resistance, but it is doubtful if any summary, covering the whole field, could be usefully attempted on this occasion. For those of you who might wish to read more generally on the subject, a number of papers might be cited, *e.g.* by Marshall Ward and Appel among earlier writers and more recently by Brooks and Walker. To the last mentioned I would specially refer you for a good and comprehensive catalogue of the types of relationship shown in parasitism.

I propose therefore to restrict the scope of my remarks to physiological aspects of parasitism, and it is for this reason that I have introduced the word "mechanism" into the title. Parasitism will be considered merely from chemical and physical points of view, and obviously one can deal only with those types of parasitism which have so far proved to be amenable, in some degree, to physiological analysis. This in itself is a very considerable restriction, and I shall now proceed to indicate more specifically certain parts of the subject which, though they may possess very great interest or importance in other respects, do not call for treatment here.

The obligate type of parasite, of which perhaps the most familiar example is *Puccinia graminis*, has always been looked upon as possessing special interest, and rightly so. The parasite-host relationship may be strikingly different with strains of the parasite which are scarcely distinguishable in any morphological respect, or again the same fungal strain may show very different effects on certain varieties of the host plant. The facts are well known to botanical readers and need only be summarised briefly.

In one case, where the strain of the fungus is brought into contact

with the right variety of host plant, the former proceeds, under suitable conditions, to send haustoria into the cells of the latter and to establish what is called a symbiotic relationship, at least for some time. That is, both the parasite and the invaded part of the host continue to thrive. There may even be, and often is, a stimulation of the host tissue showing itself in a more vigorous metabolism, as exemplified by a greater richness of contents than in the normal uninvaded cells or by a restarting of growth. The invaded cell and perhaps also uninvaded cells in the neighbourhood may enlarge abnormally or may even begin to divide. In this way arise the galls which are more or less characteristic of this type of parasitic relationship.

A very different sequence of events may be shown when a specialised parasite attacks a variety of the host which is somewhat resistant. Up to a point the process of invasion is the same as in the preceding, but from about the time when haustoria are pushed into the host cells differences arise. The haustoria are typically fewer in number and, so far as one can judge from microscopical appearance, do not seem to function vigorously. More interesting, however, is the reaction of the host tissue. The invaded cells and others nearby are soon killed, with the result that the parasite becomes hedged round by a zone of dead host tissue. As it so happens that this type of parasite can grow only on cells which are actually alive, no further progress is possible. Thus arises the curious position that the resistance to attack of the plant as a whole is based on high susceptibility ("hypersensitiveness") of its individual cells to the action of the parasite, as is shown by their being rapidly killed when invaded.

A third type of relationship has been described in which a specialised parasite is brought into contact with a plant widely removed botanically from its normal host. In such a case, the hyphae of the parasite may freely enter the intercellular spaces of the plant but they do not succeed in forming haustoria. At some stage or other the invading hyphae are killed, possibly by the action of some toxic exudation from the host cells which on their part remain unaffected.

Any attempt to study the physiology of the type of parasite which has just been described comes up against the difficulty that the highly specialised parasite cannot, so far as is known, be cultivated on any artificial medium. A decoction even of the plant which it parasitises vigorously is no more suitable for the purpose than is plain water or any other medium. A study of the metabolism of such a fungus is thus extremely difficult inasmuch as the only known substrate—the living plant—is highly complex. With fungi which are amenable to cultural treatment, one can at least begin operations with a medium of known and relatively simple composition, and however complex the changes brought about by the fungus, results are obtainable up

to the limits set by chemical technique. On the basis of these results one can attempt to interpret the behaviour of the fungus in its capacity of parasite. For the reasons stated, this line of deduction cannot even be begun with such a parasite as *Puccinia graminis*, so that we are limited to such information as is obtainable by cytological study. While the appearances presented are undoubtedly interesting, it is more than doubtful if the cytological method can ever lead to an understanding of the physiological processes involved. Interpretations in physiological terms can be and have been put forward, but these are nothing more than guesses supported by analogy with better known instances. One may plausibly postulate toxins or enzymes to explain one effect or another, but no direct evidence for the existence of these has yet been produced. Again, with reference to the marked specialisation of parasitism shown, it has been suggested that nutritive selection of particular isomeric forms of starch or protein is the underlying factor, but this is mere speculation. At the moment therefore the physiology of the specialised parasite is practically unknown, nor does there seem to be much hope of progress in that direction until someone discovers just why artificial media are useless for the growth of that type of fungus. Presumably the elusive substance is some intermediate and labile product of carbon—or nitrogen—assimilation, so that the clue should by and by be provided by the plant physiologist. It is clear therefore that the highly specialised or obligate parasite may be largely left aside so far as the present discussion is concerned.

To go now to the other end of the scale, there is a whole group of effects which are more correctly described under the heading of "disease escape" than of real resistance. Certain plants or plant varieties do not in practice suffer from such and such a disease though in reality they may be just as susceptible as others which do suffer. The point is that either from some cultural practice or from something in the habit of the plant which makes it difficult for the parasite to come into effective contact with the host, the conditions are rendered unsuitable for attack. A few of the familiar illustrations may be cited. Early potatoes may be as susceptible to blight as many of the main-crop varieties; yet blight is not in general a problem where the former are concerned, as they are removed from the land before the blight organism is normally prevalent. Again both cos and cabbage types of lettuce are susceptible to attack by the grey-mould fungus, *Botrytis cinerea*, and both may in fact be destroyed in the seedling stage over the winter or in early spring. During a normal summer however the damage to cos types is negligible whereas cabbage types may from time to time be seriously affected. This difference in response is undoubtedly correlated with the different growth habits of the two types, the large spreading leaves of a cabbage

lettuce, which are closely appressed to the ground, forming a kind of natural moist chamber which is very favourable to germination of the fungal spores with subsequent attack at the collar region. Similarly the presence of bloom on various grasses, of hairs, etc., may prevent the wetting of a plant surface after rain and thus remove one of the factors which is necessary for the initiation of attack. Features of such a kind, though they may be of great practical value, and though the mechanism concerned may be quite well understood, are not relevant to any discussion of real resistance.

A third aspect of resistance, viz. its genetical behaviour, is of very great theoretical and practical importance and has led to an enormous amount of detailed experimental work. Diseases due to specialised and non-specialised parasites have been studied from this point of view, but in general the data are not of the kind which can be interpreted in physiological terms. This very extensive field of study must therefore also be omitted here.

I now come to my subject proper. Assuming that all three factors which lead to disease are present—viz. fungus + plant + suitable environmental conditions—what means does the fungus adopt to enter and parasitise the plant, and conversely by what means does the plant attempt to prevent it from doing so? I shall attempt to dissect the process of successful attack into a series of stages which will be dealt with one by one. As I have been concerned for some years in research upon these matters, I shall endeavour not merely to state what views have been held or are now held on the various topics but to indicate as far as possible where further work is called for and more especially where it is feasible to make advances with the technique available at the moment. In other words I shall examine the subject as a field for further research.

Mechanism of penetration

The first point that arises is—does the plant exercise any inducement to the fungus to enter or is entrance merely accidental? The question of a possible directive influence, due to chemical substances, upon the movement of motile cells was first taken up by Pfeffer some fifty years ago and later studied by his student, Miyoshi, with special reference to the growth of fungal germ tubes. The latter worker makes out what appears to be a complete case for a directive chemical stimulation ("Chemotropism"). Germ tubes are described as passing through minute openings in artificial films or through permeable membranes or into glass capillaries, the attractive agent in each case being the appropriate concentration of some chemical placed on the opposite side of the membrane or in the capillary tube. Unfortunately Miyoshi's work is largely refuted, in matters of fact, by researches carried out later by a number of investigators, *e.g.* Clark and Fulton,

who failed to find much evidence for the positive chemotropism of Miyoshi, but substituted instead a negative chemotropism or growth away from certain products made by the fungus itself. The latest detailed work on the subject, by Graves, found some truth in both the earlier views, viz. that both types of tropism can be demonstrated but that the negative tropism to fungal metabolic products is the greater effect. It is in fact abundantly clear, even from internal evidence, that some of Miyoshi's conclusions are highly overdrawn. Graves's paper is the latest of any importance on chemotropism of fungal hyphae, and, though the subject cannot be considered as adequately worked out yet, we must accept his conclusions as the best available for the time being.

When we come to consider how far the phenomenon of chemotropism plays a part in the initiation of parasitism, we find considerable divergence in the views expressed. Massee in an early paper accepted Miyoshi's results in their entirety and proceeded to construct a physiology of fungal attack on this basis. According to his view, when chemotropic substances diffuse out of the host tissue on to the surface, fungi enter; when there is no such diffusion, there is no entry. Specialised parasites are those which respond to a special substance, and a non-specialised parasite responds to nutrients in general. Now there is no doubt that such an interpretation is very wide of the mark, and it is sufficient to point out, as was pointed out long ago, that fungi will often enter a host which they are quite unable to parasitise. Penetration is merely one of a number of steps which lead to parasitism.

By other writers the chemotropic theory has been applied with greater reserve to the explanation of parasitism. Fulton suggests that under conditions of a drying atmosphere, the germ tubes of fungi may be attracted by the turgid cells underlying the stomata ("hydrotropism"). The negative tropism of hyphae to each other may, according to Graves, be responsible for the ramification of the fungus through the host tissue. In plant pathological papers generally, chemotropism is usually assumed or suggested as a factor in fungal growth, without the production of any fresh evidence bearing on the point.

In examining the applicability of these theories of chemotropism to the initiation of parasitism, it will be well to distinguish the two modes of entry available, cuticular and stomatal. With regard to the former, it is quite plausible that a fungal germ tube growing over the surface of the plant might be unequally stimulated on its near and far sides by some chemical diffusing out of the underlying cells. In response to this unilateral effect, it might be induced to grow towards the source of the stimulating substance. On the other hand, experiments have shown quite definitely that penetration of artificial

or natural membranes by the germ tubes of *Botrytis cinerea* readily takes place no matter what the original distribution of the nutrient substances might be, *i.e.* the fungus penetrates equally well with or against the gradient of chemotropic substance, or if there is no gradient at all. Miyoshi's and Massee's observations, that penetration of certain plants did not occur when the underlying tissue was injected with water but that it did so when a sugar solution was used, can be explained on grounds other than chemotropism, as will be shown later. It is clear therefore that chemotropism to stimulatory substances is not a necessary factor for cuticular penetration, though it has not been disproved—and it would require a very careful quantitative examination to disprove it—as a contributing factor in the process.

The application of Fulton's negative tropism to the explanation of cuticular penetration is a physical impossibility. At first glance it might seem that the accumulation of staling products in the infection drop would cause the germ tubes to turn away from the region of high concentration—viz. the infection drop—to a region of no concentration, viz. the underlying host cells. This, however, is begging the question. The response of the germ tubes can be determined only by conditions within the infection drop, and there is no reason why there should be a lower concentration of staling substance on the side next the cuticle than on the side away from it. In fact, on principles of diffusion, the reverse is more likely, and one would expect the hyphae, if subject to this negative tropism, to turn away from the cuticle.

As regards stomatal penetration, very little of the work of Miyoshi, Fulton, or Graves appears to be relevant. The perforated mica plate, which has been used so much in researches on chemotropism, is presumed to furnish a working model of the plant epidermis with its stomata. An important difference however is that the substomatal chamber is normally full of air, so that there is no means for the outward diffusion of sugars, salts, etc., which are the presumed chemotropically active substances. If there is any chemotropic influence concerned, it must arise from some volatile substance. Balls has in fact suggested that the germ tubes of rust spores pass through the stomata of the host plant as the result of a positive tropism to water vapour.

Chemotropic theories being thus unsatisfactory, one has recourse to the alternative view, which has also been suggested from time to time, viz. that the stimulus to penetration is a contact one, at least as regards entry through the cuticle. The theory of contact-tropism has the great disadvantage that it is very difficult to explore experimentally, and in the main it is rather based on a negative, *i.e.* the inadequacy of the chemotropic theories. There is, however, some definite evidence in its favour. Thus a germ tube of *Botrytis cinerea*,

when on the point of penetrating the cuticle of a plant, produces a slight swelling or "appressorium" whereby, through partial gelatinisation of the fungal wall, the tip of the hypha is firmly attached to the surface of the host. From this appressorium the penetrating hypha is put out through the cuticle in the form of a fine peg or thread. Now when a germ tube of the same fungus is grown on a glass slide, a whole series of such appressoria may be formed. There is of course no penetration, but it is reasonable to suppose that each appressorium represents an attempt to penetrate, that after a time the fungus resumes growth but soon tries again, and so on. There can be no question of a chemotropism in such a case.

The adoption of a theory of contact-tropism in preference to a chemical one does not mean that chemical factors are of no importance in connection with the stimulus to penetrate. Any particular fungus may react differently according to the medium in which it is growing, *i.e.* chemical factors may decide whether appressoria are or are not formed in response to a contact stimulus. In the absence of any definite information on this point and on the further point as to whether response to contact is in any way influenced by the physical nature of the surface touched, the question of tropisms may be left with the statement that so far the theory of contact-tropism is the only one to which damaging objections cannot for the present be raised.

As regards entry through the cuticle, the further point now arises as to the mechanism of the actual process of penetration. Here again two theories, a mechanical and a chemical, hold the field. According to the latter some substance is excreted by the fungus which softens or dissolves the cuticle. The difficulty is that no one has demonstrated the existence of such a chemical substance. The enzyme pectinase which is secreted by many fungi and which actively dissolves certain cell wall constituents is, so far as is known, quite inert when brought into contact with a cuticularised surface. It is just the outermost layer which is unaffected, but this is all-important. There may also be occasional plant parts which are not sufficiently protected, but the rule is overwhelmingly as already stated. Some evidence in favour of a chemical agent has been adduced from cytological studies, *e.g.* from the appearance of some kind of staining reaction below the cuticle in the neighbourhood of a penetrating hypha, and at a time when penetration has not yet been effected. Apart from the very considerable risk of misinterpreting the exact sequence of events—for the earliest phase of penetration is very difficult to fix properly—there is the criticism that any such staining reaction is not evidence bearing on the question of softening or dissolving of the cuticle.

One has therefore, as before, to fall back upon a theory of mechanical penetration. While it is impossible to outline the mechanics

of the process, a considerable amount of evidence can be adduced in favour of this view. Thus it has been shown that fungi are able to penetrate a variety of membranes—*e.g.* collodion, paraffin wax, gold leaf—which in all probability they are unable to attack by chemical means. My own experiments with membranes of formalised gelatine of graded hardness can only be interpreted on the mechanical theory. Brown and Harvey's work on the penetration of *Eucharis* leaf by *Botrytis cinerea* showed that the mechanical resistance to penetration of an epidermis is conditioned in part by the hydrostatic backing of the cells behind, and again the results were strongly in favour of the view that the mechanism of penetration is physical.

The *a priori* objection, that it is incredible that such a soft thing as a fungal germ tube can penetrate such a hard thing as a plant cuticle, has no justification in fact and is fully met by a recital of the types of membrane which fungi have been shown to penetrate. The germ tube, it may be remembered, does not penetrate as such but in the form of an extremely fine peg, which may subsequently enlarge to more or less normal diameter when the mechanical strength of epidermis + cuticle has been largely destroyed by enzymic digestion from within, *i.e.* after the enzymically impermeable cuticular barrier has been passed.

Quite a number of observers have supported the mechanical theory of penetration from careful microscopic work, but of course it is not impossible that some fungi may have some chemical means of carrying out or perhaps assisting in the process. Up to the present however no satisfactory evidence of the existence of a cuticle-dissolving enzyme is forthcoming.

The mechanical theory of penetration in its simplest form would entail the possibility that parasitic fungi could be arranged in a series as regards power of penetration and conversely that host epidermes could be similarly graded according to their intrinsic mechanical resistance. It has in fact been shown, by the use of membranes of graded hardness, that *Botrytis cinerea* has a greater capacity to penetrate than has *Penicillium glaucum* which again is more active in that respect than *Rhizopus nigricans*. This series is in agreement with the parasitic tendencies of the three fungi. Further research however may show that the matter is not so simple and that such a state of affairs as is indicated in the following scheme may exist:

	Host *A*	Host *B*
Fungus *a*	+	–
Fungus *b*	–	+

where + indicates penetration (not necessarily leading to macroscopically visible parasitism). If such a relationship were established the simple mechanical theory would require modification.

Successful penetration means that a chain of effects has been completed. First of all the fungus has been stimulated to attach itself to the host surface, and then to attempt to send in a process at some point of the area of contact. Finally there is the physical act of penetration. Whether the stimulus which produces attachment is the same as that which leads to penetration is not known. From these considerations, it is clear that the theory of mechanical penetration is sufficiently elastic to allow of the process being selective, as envisaged in the scheme above. The nutritional relationships, to be discussed in the following paragraphs, would also need to be borne in mind. A critical study of the whole process is unfortunately still lacking.

A discussion of the mechanism of penetration is incomplete without some consideration of the sources of energy available to the fungus whereby it is able to reach the underlying host tissue. The spores must germinate with sufficient vigour and speed to enable entry to take place while favourable environmental conditions (presence of dew, rain, etc.) prevail. Three possibilities come up for consideration here.

The spore itself may contain the necessary food reserves. Germination studies in distilled water show that there is considerable variation among fungi with regard to the capacity of the spores to germinate on their own resources. Again, spores of the same fungus respond very differently according to age or to the manner in which the fungus has been grown. Thus, in a general way, young spores germinate quickly and evenly, with stout germ tubes, and to a high percentage. As they become older ("attenuated by age"), the percentage germination diminishes, so that a sample field shows some spores with fairly long thin germ tubes and others which do not germinate at all. Spores of this type may still be able to germinate vigorously and fairly evenly if supplied with a trace of food. It is obvious that spores are capable of greater parasitic activity at their period of optimal germination than at other times.

Frequently however the fungus, whether as spore or as mycelium, which is in contact with the surface of the host plant, has access to extraneous food supplies, and that in a purely passive manner. Soil fungi have the benefit of food substances present in the soil solution. Even on subaerial parts, where the fungus is in contact with initially pure water such as dew, it does not follow that that water remains pure throughout. It can be shown very simply that appreciable exosmosis takes place from many living plant tissues, through the cuticle, into drops of water laid on the surface, and that this process goes on independently of any fungal spores which may be present in the water. The effect of this exosmosis is in many cases to increase the vigour of spore germination; in others there is a repression or

even inhibition. Though the amount of chemical substance so rendered available to the fungus may actually be very small, it is enough to affect markedly the vigour of germination.

The third possibility rests on the statement of de Bary, in his pioneer researches on *Sclerotinia*, that certain parasites are able to kill underlying cells of the host before penetration has actually been effected, and by that means to have access to soluble food substances which diffuse out from the killed cells. De Bary is responsible for the view that parasites of the facultative type invade only after previous saprophytic feeding. The hypothesis of "killing in advance of penetration" is a corollary to the general view. Neither of these has been fully borne out by later work. The necessity for saprophytic nourishment as a preliminary to parasitism is definitely an overstatement. It is more correct to say that with spores of low inherent vigour, saprophytic nourishment materially enhances the ability to parasitise. The claim that certain parasites kill in advance of penetration has also not been substantiated by more recent critical studies. The subject is one of considerable technical difficulty, even with modern cytological methods, and it is not surprising that de Bary somewhat misinterpreted the sequence of events. From his own writings it is evident that de Bary was not satisfied with his conclusions, and the acceptance of the latter by other workers (*e.g.* Nordhausen) led to some irreconcilable results. It is obvious that the theory of killing in advance of penetration requires the excretion by parasitic fungi of some toxic substance which is capable of diffusing through the plant cuticle. This subject will be discussed later in a somewhat different connection; in the meanwhile it is sufficient to state that no satisfactory evidence of the existence of such a substance has been advanced. Until such time as the necessary evidence is forthcoming, the theory under consideration may be discarded.

The protection afforded to a plant by its outer layer (cuticle or bark) is undoubtedly of very great importance. Many plants are immune to attack from certain fungi only so long as the surface is intact. In such a case the fungus is spoken of as a "wound parasite." The susceptibility of some young structures (young leaves, meristematic regions) to attack while the older mature parts are resistant has similarly been ascribed to the strengthening of the cuticle as maturity increases. Familiar examples are seen in the incidence of apple rust and apple scab. The greater resistance of mature plants of cereals as compared with that of seedlings to attack by the uredospores of *Puccinia graminis* is not relevant in this connection since penetration is through the stomata. Some question of internal resistance is therefore concerned, and as regards the two apple diseases cited, it might be added that, though the mode of penetration is cuticular, internal factors of resistance may likewise be operative.

Internal resistance

Perhaps undue attention has been paid to penetration as this is not, after all, the most important or the most interesting phase in the establishment of parasitism. As has been already stated, fungi may often enter within the tissue of a plant without attack ensuing. One may therefore put such questions as the following. Why is it that, if any parasite is put into any plant at random, *i.e.* all questions of penetration being side-tracked by placing the potential parasite into a wound, attack does not develop? Why is a so-called saprophytic fungus unable to parasitise? Or, to take a more particular example, why is a parasitic fungus able to attack under one set of conditions and not under others? These questions obviously cover a wide ground, and make up in fact the fundamental problem of plant pathology.

As has already been noted, the only rational method of constructing a physiology of parasitism is to study the growth activities of fungi on media of known composition and to attempt to apply the results to the more complex case where the fungus is growing on a living plant. Before turning to a consideration of the main features of fungal metabolism so far as they may be reckoned to bear on parasitism, it will be well to point out what is the essential difference between an artificial medium and a living plant as substrates for fungal growth. Apart from the possibility that any particular plant may be of unsuitable composition for growth of the fungus, there is the main fact that the food contained in a living plant is not immediately accessible to the parasite. It is more or less effectively held up behind the double barrier of a mechanically strong cell wall and a relatively impermeable plasmatic membrane. It is now opportune therefore to consider what mechanism a parasitic fungus possesses for breaking down this double barrier.

First of all there is the power of mechanical penetration to which reference has already been made. This property might conceivably enable a parasitic fungus to force a way through the tissue of a plant and it is not impossible that the mere disturbance due to the physical presence of the hyphae within the cells might lead, in a manner that is not understood, to the death of the latter. In this way the whole resistance of the plant might be broken down by mechanical means only. Then there are chemical agencies. Fungi in the course of their growth produce a variety of chemical substances—acids, enzymes and it may be other types of substances—capable of attacking plant cells. That such substances are in fact produced and excreted by the parasite into the tissues of the host is very obvious in some cases. Microscopic examination shows a more or less pronounced action on the host cells in advance of the hyphae of the parasite, this action taking the form of a disorganisation or rotting of the cell wall sub-

stance and a killing of the protoplast. The resistance of the tissue is broken down by this means and such a parasite is in effect living saprophytically on killed parts of the plant. It is just this feature, viz. the action in advance of the hyphae, that makes possible the physiological analysis of the mode of attack of the facultative parasite. The nature of the active substance concerned may now be considered in some detail.

Apart from special cases, *e.g.* wilt diseases, in which the active substance has been claimed to be a nitrite, chief attention has been paid to organic acids, more specifically oxalic acid, and the cell wall dissolving enzyme pectinase (or cytase of earlier workers). Almost every conceivable view has been expressed with regard to the relative importance of these two substances. At one extreme, oxalic acid secreted by the parasite has been considered to be responsible both for the dissolving or macerating action on the cell walls and for the killing of the protoplasts. More usually the action on the cell wall has been ascribed to the enzyme and the toxic action to the acid. At the opposite extreme, both actions have been ascribed to the enzyme.

The evidence relative to the oxalic acid theory will be given first. This acid is a frequently occurring product of fungal metabolism. It is formed in greater quantities by some species or strains of fungi than by others, and most strikingly by some strains of *Aspergillus niger*. Even with a suitable fungus, the amount of oxalic acid formed varies very markedly with the conditions of culture. Media rich in glucose and peptone are specially recommended and the temperature should not be allowed to go above a certain point otherwise the oxalic acid is liable to be completely respired to carbon dioxide. Maximum yields are obtained only when the conditions of culture are such that any oxalic acid formed is immediately removed from the scene of the reaction, *e.g.* by precipitation with a soluble calcium salt. It is important to note this point, since the high figures which have been quoted by some writers for oxalic acid production do not always distinguish clearly between soluble and insoluble oxalate and between soluble oxalate and oxalic acid.

Oxalic acid as such is a fairly active poison to plant cells. Whether this property is due entirely to its strength as an acid (*i.e.* to H-ion concentration), as has been claimed, or in part to molecules of undissociated oxalic acid, is not clear. The oxalate ion has certainly very little toxic effect, as is shown by the relative harmlessness of neutral soluble oxalates. As regards any action of oxalic acid upon the cell wall substance, this is due to H-ion concentration, and only becomes appreciable when the latter exceeds a certain value.

The best known supporter of the oxalic acid theory is the American worker Smith who claimed that both the dissolving and toxic actions

of *Botrytis cinerea* on lettuce tissue could be explained on this basis. The evidence offered is open to serious objections. There is in the first place no proof that a sufficiently high concentration of oxalic acid is secreted by the fungus, the author relying on a statement of de Bary which had reference to the fungus *Sclerotinia Libertiana* and which furthermore is misinterpreted. De Bary's statement refers to total oxalate, but Smith construes it as oxalic acid.

A further important objection to the oxalic acid theory is to be found in Smith's own results. Even when a solution of the acid, sufficiently concentrated to cause dissolving and killing effects on the tissue, is used, the action does not reproduce that of the fungus. The tissue parasitised by the fungus becomes brown, whereas the acid has a bleaching effect. Smith's interpretation of this difference cannot be accepted. On the contrary the mere fact that oxalic acid interferes with the oxidase colour reaction of the killed tissue proves conclusively that that concentration of acid cannot be present during attack by the fungus.

More recently oxalic acid has been advocated by Higgins as the active principle in the parasitism of *Sclerotinia Rolfsii*. Here again there is, apart from obscurities on critical points, no proof that a toxic concentration of *oxalic acid* is produced by the fungus under conditions comparable to those which obtain in the neighbourhood of the invading hyphae.

The objections to the oxalic acid theory just given do not exhaust the list. It has been pointed out, for example, that if secretion of acid is the factor responsible for parasitism, such a fungus as *Aspergillus niger*, which is particularly notable in this respect, should be an active parasite—which in fact it is not. I do not consider that this objection is necessarily insuperable, or at any rate, as I shall show later, the protagonist of the enzymic theory has very much the same difficulty to explain away.

With some fungi at least there is definite proof that the active principle is not oxalic or any other acid. Thus the parasitic action of *Botrytis cinerea* can be imitated exactly by an extract of neutral reaction, which furthermore contains no trace of an oxalate. Again many parasites (*e.g.* species of *Fusarium*, *Pythium de Baryanum*, certain plant pathogenic bacteria, etc.) have a strong tendency to develop an alkaline reaction in growth and in fact induce an alkaline or at most a faintly acid reaction in parasitised tissue.

Where a distinctly acid reaction is produced during fungal invasion or where the parasitism of a fungus is favoured by the addition of an acid, it does not follow that the acid is the agent primarily responsible for attack of the tissue. One may equally reasonably suggest that acidity favours the action of the active principle, which is another substance altogether.

My own view with regard to the importance of oxalic acid in connection with parasitism is that in no case has satisfactory evidence been brought forward, while in many others there is convincing evidence against it. It is insufficient to point out that such and such a fungus produces large quantities of this acid when grown in culture for several weeks on media of specially arranged composition, for example on media of high sugar content. It must be remembered that spores of a parasitic fungus when placed in water on the surface of a plant normally begin to attack within a day or so, and it is under these restricted conditions that the secretion of an effective concentration of oxalic acid must be demonstrated. As the toxicity of oxalic acid appears to be due mainly to its acidity, the technique involved is simple. No clear proof along the lines indicated has yet been given.

There remains the alternative theory that the enzyme pectinase is the active principle of parasitism. So far as concerns its occurrence, there is good *a priori* evidence. Its formation has been demonstrated for many fungi, in my own laboratory for some dozen species which have been studied in this connection. The difficulty here is rather of another kind, viz. that this enzyme is also secreted by mere saprophytes, and that there is no correlation between the amount of enzyme which can be demonstrated under standard conditions and the parasitic vigour of the fungus. This point will be taken up more fully later.

It appears to me to be obvious that where definite rotting of the parasitised tissue occurs—and this effect is shown with greater or less distinctness with the vast majority of parasites of the facultative type—the enzyme pectinase must be present. The majority of workers from de Bary onwards have accepted this view. The enzyme has been considered to be responsible for the attack upon the host cell walls, while the nature of the toxic principle has been left open. The most detailed examination of this point was that carried out by myself some years ago, where it was shown for the fungus *Botrytis cinerea* that the macerating and toxic principles, if they are different, are both colloidal thermolabile substances which are strikingly similar in their response to *p*H concentration, to deactivation by heat or mechanical agitation and in their diffusive capacities through certain membranes. As was pointed out at the time, the evidence available can be interpreted in more than one way, but the simplest hypothesis is that the two manifestations of activity are due to the same substance. Certain implications as to protoplasmic structure would arise from this conclusion, but these do not concern us here. The further consideration of the enzymic theory will be taken up later.

A survey of the interplay between host and parasite when brought into intimate contact with each other may conveniently be given

from the point of view of the kind of resistance which the host may offer. I propose to distinguish five types, largely because concrete examples of each can be given. With advancing knowledge, a finer classification will no doubt be possible. The types of resistance are as before, mechanical and chemical, and the latter is further subdivisible into four categories.

(1) *Mechanical resistance*

A familiar example of this is seen in the limiting of fungal invasion by the lines of vascular bundles with their accompanying fibres (*e.g.* in grass leaves). More familiar still to plant pathologists are the various structures such as cork layers, gum barriers, callosities etc. which are formed by the host in response to wounding. That these do in fact place an utmost limit to the fungal invasion cannot be doubted, though it might fairly be suggested that in some cases at least invasion had already been stopped by some chemical factor. Whether the wound response is conditioned solely by the host or whether excretions from the fungus play some part is not known. It is not impossible for instance that some parasites may have the power of suppressing cork formation, being able by that means to parasitise the tissue throughout. The physiology of cork formation is obviously one of live interest to the plant pathologist.

A general correlation is sometimes indicated between the percentage of cell wall substance of plants and resistance to fungal disease. For example, it appears to be a fairly good rule that cultivated forms of plants are more susceptible to a variety of fungoid diseases than are their wild prototypes. As cultivation has often led to the development of soft fleshy or succulent structures, it has been plausibly held that resistance is correlated with a greater average thickness of the cell walls and conversely. More specifically it has been claimed that this factor of mechanical resistance explains the different degrees of varietal resistance of plums to *Sclerotinia* (Valleau) and of potato tubers to *Pythium deBaryanum* (Hawkins and Harvey). As both the diseases mentioned are characterised by very distinct rotting of the tissues, it is incontestable that enzymatic action is concerned. I should doubt therefore whether mechanical resistance is really operative, and would suggest that the true factor of resistance is a chemical one which is correlated with the development of thicker or more rigid walls. As fungi do possess the power of mechanical penetration, one cannot say offhand just how far the physical factor supports the chemical one, and it is probable that their relative importance varies from one disease to another. Inasmuch as plant pathogenic bacteria cannot be considered to possess any means of mechanical penetration, it is obvious that the chemical mechanism is all-important in their case, and, as the course of a bacterial disease

is essentially similar to that of a fungal one, it is perhaps safe to discount the mechanical factor, at least in any case where enzymatic action is clearly marked.

(2) *Chemical resistance*

Four types can be distinguished here, and these will be dealt with in succession.

(*a*) The composition of the plant may be such as to be unsuitable for the growth of a particular fungus. This type of resistance will be illustrated by a number of examples.

High acidity of the plant sap has been given as the factor which protects certain plants or plant parts against some fungi, and there is no doubt that this is sometimes a satisfying explanation. Thus it is clear that only fungi with a high acid tolerance could parasitise such acid structures as unripe apples or plums, and on examination one finds that *Monilia* spp., which parasitise these fruits, have a remarkably high acid tolerance. The factor of acidity has also been used in explaining the mode of invasion of certain citrus fruit parasites (*e.g. Pythiacystis*) which more or less avoid the acid succulent hairs but ramify through the central axis, dissepiments and pericarp.

It is difficult to believe, however, that acidity of the plant sap, as a factor repressive to fungal growth, can have any wide application. The acid concentration of the vast majority of plant tissues is well within the limits for good growth of most fungi. While high acidity of a particular plant would restrict parasitism to such fungi as preferred a highly acid reaction or at least tolerated it, with perhaps a tendency to reduce the amount of acid and thereby to create more favourable growth conditions, this factor is quite inadequate to explain the resistance of a plant with more usual composition. More particularly, it offers no basis on which to construct a theory which would explain the degree of selectivity shown by the facultative type of parasite. In passing it may be noted that all attempts to explain the specialisation of obligate parasites such as rusts on the basis of fine differences in *p*H concentrations of the host plants have similarly ended in failure.

The presence in the plant of particular substances which act as poisons or inhibitors to fungi has also been cited as explaining resistance to attack. Such substances are oils, esters, tannins, etc., either present as such or produced in the lesion in response to wounding. It is well known, for example, that the volatile principle of onion bulbs is highly repressive to the growth of fungi in general, while those fungi which do parasitise onion show relative tolerance. In this connection may also be quoted the observed association of resistance in some plants with the presence of a particular colour. That the agent responsible for resistance is not the pigment itself but a

substance associated with it has been shown recently by workers in the Madison laboratory. The resistance of certain coloured varieties of onion to the "smudge" fungus (*Colletotrichum circinans*) has been proved to be due to the presence of an organic substance of ascertained constitution.

Now while the search for inhibitory substances and the like has yielded some measure of success, I do not believe that any general solution of selective parasitism is to be found along these lines. The relationship to be explained is a reciprocal one, of the type indicated in the scheme already put before you (p. 18), with the symbols + and − now meaning respectively ability and inability to parasitise. If fungus *a* attacks host *A* because there is no repressive substance present in *A* whereas host *B* is not attacked because it contains such a substance, how is one to explain the behaviour of fungus *b*? One could, it is true, get over the difficulty by postulating two repressive substances to which the two fungi were unequally sensitive. While there is some degree of selective action by poisons upon fungi, the main truth is that toxicity is a fairly absolute property, so that it is more than doubtful if any satisfactory explanation is to be found on the basis of special toxic or repressive substances. I therefore look upon the type of resistance under consideration as being limited to special cases only.

(*b*) A second type of chemical resistance is seen where the composition of a plant is such as to allow ready growth of a fungus but not the secretion in appreciable quantity of the active substance. At the moment I can quote only one definite instance of this kind of resistance, viz. that of the apple fruit to various fungi. The controlling factor appears to be low nitrogen content of this fruit.

Vasudeva found that the fungus *Botrytis Allii*, which normally is not parasitic upon apples, produces definite attack if supplied with a small quantity of a variety of nitrogenous substances. From the point of view of spore germination or of mycelial development, apple extract, at any concentration from full strength downwards, is perfectly suitable for the fungus in question. The significant difference is that whereas no detectable pectinase enzyme is formed when apple extract is used as nutrient, it is very definitely present when a trace of nitrogenous substance is added to that medium. It appears therefore that resistance of the fruit is based upon its very low nitrogen content, not as repressing growth but enzyme secretion. It may be added that a slight increase of nitrogen supply likewise enhances the parasitic vigour even of a pronounced apple parasite like *Monilia fructigena*. Presumably therefore the difference between these two fungi, as regards attack of apple fruit, is that the latter produces an effective secretion of pectinase at a lower concentration of nitrogen in the substrate than does *Botrytis Allii*.

Horne has likewise shown that there is a high inverse correlation between the nitrogen content of different individual apples of the same variety and the rate of invasion by a parasitic fungus.

(*c*) The third type is to my mind by far the most important of all. The composition of the plant is such as to favour fungal growth, and also, as far as can be seen, to allow of secretion of the pectinase enzyme; nevertheless there is no attack. This may be described as the case of the average fungus, *i.e.* with no special food requirements or special sensitiveness or tolerance to chemical substances, and the average plant, *i.e.* with no special inhibitory constituent.

A particular example of this type of resistance is that of potato tuber tissue to *Botrytis cinerea**. This fungus grows vigorously on potato decoctions of widely varying strength, and on pieces of potato tuber which have been autoclaved, or steamed or chloroformed or frozen. From any one of these media a preparation can be made which actively destroys pieces of potato tissue when immersed in it. When spores of *B. cinerea* are placed in a wound on potato tissue they germinate vigorously. On the enzyme theory, every necessary condition appears to be fulfilled. Nevertheless attack is slight or negligible.

The difficulty seems to be even greater when one compares *B. cinerea*, a non-parasite of potato tuber, side by side with *Pythium deBaryanum*, an active parasite. Preparations of pectinase enzyme can be prepared from the latter fungus, but so far under much more restricted conditions than from *Botrytis cinerea*. Thus while good enzymic extracts may be obtained from cultures of *Pythium* on living or dead potato tubers, cultures on potato decoction give inactive or very feebly active preparations. On the latter medium *Botrytis cinerea* gives very active preparations, either in the medium itself or by extracting the young mycelium.

The readiness with which a fungus secretes the pectinase enzyme does not therefore give any reliable index of its parasitising ability. The same difficulty has already been pointed out by a number of workers. Thus Harter and Weimer could find no correlation between the parasitic vigour of different species of *Rhizopus* and their capacity to furnish active enzymic solutions under standard conditions. The same conclusion was reached by Paul for a number of strains of *Botrytis cinerea*.

A satisfactory explanation of the basis of resistance in the case under consideration thus gives a critical test of the enzymic theory of

* As the host-parasite relationship is probably somewhat delicately balanced, it is not unlikely that some strains of *Botrytis cinerea* may be able to attack potato tissue under a wider range of conditions than do the strains which have been used in my laboratory.

In the remainder of this paper I shall have occasion to refer frequently to a number of unpublished researches which are in progress, chiefly by M. P. Hall, K.P.V. Menon and M. Fernando.

parasitism. While it is not yet possible to give a complete story, even for a single fungus and host, several points have emerged in recent work which make the difficulty less formidable.

Up till fairly recently certain assumptions have been made with regard to fungal pectinase, and these now require considerable overhauling. From my own work it was known that pectinase is secreted (and excreted) from the earliest phases of spore germination onwards; that under a given set of conditions the quantity present in a culture increased up to a maximum and then slowly diminished. In the lack of any better information, one assumed that there was a certain proportionality between vigour of growth and rate of excretion of the enzyme. Another assumption was that pectinase had the same properties under all conditions and that the pectinase of one fungus was the same as that of any other, though as a matter of fact I knew long ago that the pectinase of *Botrytis cinerea* had very different properties from the pectinase (=cytase of Brown and Morris) of the germinating cereal grain. Further work has shown that everywhere there are greater complications.

The activity of the enzymic solution obtained from a fungus under standard conditions would be a measure of parasitic vigour only in so far as there was some proportionality between the rates of enzymic excretion under different nutrient conditions. To refer to the two fungi quoted above, if *Botrytis cinerea* produces a stronger enzymic solution when grown on potato extract than does *Pythium deBaryanum*, is one justified in assuming that the same applies when the fungi are placed on the cut surface of living potato tissue? There is an increasing body of evidence to the effect that the quality and quantity of nutrients has an important influence on the amount of enzyme excreted. If has recently been shown that, over a certain range of concentrations, there is a negative correlation between amount of growth and enzymic excretion, the controlling factor being largely the carbon/nitrogen ratio of the medium. When the ratio is very high there is luxuriant growth but very feeble excretion of enzyme; when the ratio is very low, the amount of growth may be negligible but abundant enzyme is formed. A somewhat similar point has already been referred to in *Botrytis Allii* in relation to apple fruit. These findings—that the nitrogenous constituent has a markedly intensifying influence on secretion of pectinase—fall into line with general experience that nitrogenous manuring typically increases susceptibility to disease.

The quality of carbonaceous food appears also to be of importance. Thus *Pythium deBaryanum* produces negligible or considerable amounts of enzyme when grown on potato decoction or tissue respectively. There is here a suggestion that the occurrence of pectic substances in the substrate intensifies the production of pectinase. Harter and

Weimer likewise found that the presence of pectin in the medium intensified the secretion of pectinase by species of *Rhizopus*. The work of Dickson and collaborators on the resistance of wheat seedlings to *Gibberella Saubinetii* appears to be capable of a similar interpretation. It was found that under one set of conditions the seedlings developed cell walls of a more definitely pectic nature than under other conditions. The former were susceptible to blight and the latter were not.

A first point then is that there is some specificity in the secretion of pectinase, and the precise conditions have obviously got to be worked out for each particular fungus before any valid quantitative comparisons can be made.

A second point is that the detailed properties are not the same for pectinase as prepared for different fungi or even as prepared under different conditions from the same fungus. Chona showed that whereas the enzyme of *Botrytis cinerea*, extracted from germinated spores, was favoured in its activity by an acid reaction but was highly sensitive to the presence of certain salts, the enzyme of *Pythium deBaryanum* had its optimal activity in an alkaline medium and was relatively tolerant to the salts in question. Later Menon demonstrated definite differences between pectinase enzyme as prepared from *Monilia fructigena* grown on different media.

The latter evidence tends to discount the view that there are possibly an indefinite number of types of pectinase. A more plausible hypothesis is that it is the same pectinase in all cases, but that the enzyme has some of its properties modified by association with substances in the medium. As the differences quoted above persist after the enzyme has been purified to some extent by precipitation with alcohol, adsorption phenomena are suggested. Work in progress is giving results in conformity with the provisional rule that the pectinase enzyme is less sensitive to a particular substance when secreted in the presence of that substance. In accordance with this rule the enzyme is favoured by an acid or an alkaline reaction according as the conditions of culture are such as to tend to acidity or alkalinity as growth of the fungus proceeds. Much further work will be required before it is seen how far this rule applies and what are its limitations. Its importance lies in this, that to some extent at least a fungus is able to adapt its enzymic mechanism to deal with a plant containing substances which might appear to be antagonistic to the action of the enzyme, if the latter were used in some standard form.

A third point, which may not be independent of the last, is that, even when active enzyme is known to be present, there may be negligible attack of a susceptible tissue under certain conditions. An illustration will make this clear. A sample of *Botrytis* enzyme is tested by immersing standard discs of potato tissue in it and found to be very active. When drops of the same preparation are placed

on the freshly cut surface of a potato tuber, they are found to be quickly absorbed by the tissue (which has a certain avidity for water, even when normally turgid) and very little rotting is produced. If however the tissue is previously injected with water so that it is completely turgid, drops of the enzyme solution produce very considerable rotting. In this connection it is very illuminating to note that the fungus itself behaves similarly, viz. that when its spores are placed on subturgid tissue there is no attack, whereas when the tissue is fully turgid attack is very definite. The similarity in the behaviour of fungus and enzyme gives strong ground for the belief that the enzyme is in fact the essential part of the parasitising mechanism.

The failure of *Botrytis cinerea* to attack ordinary potato tissue is now somewhat understandable. Even if any enzyme is formed under these conditions—which is not certain—it would fail to act, in accordance with what has been said above. What happens to the enzyme when the tissue absorbs water from the drops laid on, and why it fails to produce any rotting are points that require further study. A point of more immediate importance, however, is to explain why *Pythium deBaryanum* or *Phytophthora erythroseptica* under the same conditions produces an enzyme which *does* attack the tissue. As a working hypothesis I would suggest that the difference is to be sought in the other metabolic products of the fungi. It has been shown that a factor making for resistance is the capacity of the living tissue to absorb water from the neighbourhood of the fungus, thus paralysing in some way the enzyme. Presumably there is some substance or substances formed by *Pythium* which counteract this absorptive effect. Further work will show how far an explanation can be found along this line.

The water exchange between fungus and host is probably a factor of first class importance in conditioning parasitism. It is of course common knowledge that moist conditions are necessary for the initiation of attack, but one usually assumes that the moisture functions merely by allowing germination and penetration. Once the fungus has become established inside, moisture conditions are supposed to be less important. There are numerous observations, however, which fall into line with the hypothesis that a turgor deficit within the tissue confers resistance. This has been shown, for example, in quantitative studies of the rate of attack of apples by *Monilia fructigena*. Conversely it has been found by various workers that many fungi attack a wider range of plants under laboratory conditions than in nature. The unnaturally humid conditions which are set up in laboratory experiments may well afford the explanation. Again many seed-borne fungi show a behaviour which could best be explained in terms of moisture relationships. If conditions are such that the plant is turgid, attack progresses; if there is subturgor, the fungus, though it may

have entered, is unable to progress to the extent of making a macroscopically visible lesion, but remains dormant until such time as sufficient turgor is again established. The limited spread of the shot-hole type of lesion and even of a disease like apple scab would be explained on the same basis. I would also suggest that the difference between a soft rot and a hard rot rests upon a different water balance between parasite and host in the two cases. The soft-rotting organism retains in its surroundings sufficient water to enable enzymic decomposition to proceed to completion whereas in a hard rot enzyme action is arrested at some intermediate stage. Viewed in this light, a hard-rot indicates a less developed parasitic mechanism than does a soft rot, and accordingly I would consider the following list of parasites as forming a series of increasing parasitic capacity in relation to potato tissue: *Botrytis cinerea*, *Phytophthora infestans*, *P. erythroseptica*, *Pythium deBaryanum*.

(*d*) A fourth type of chemical resistance is that in which the active principle of the fungus is unable to affect the tissue of the plant. Certain mosses and hepatics have been found to possess this type of resistance to the fungus *Botrytis cinerea*. These may be overgrown by the mycelium of the fungus or may be heavily sprayed with spores under conditions favourable for attack, without a trace of injury appearing. Similarly an enzyme solution of the fungus produces no effect on these tissues. One may look upon this case as illustrating a more fundamental and absolute type of immunity than anything discussed above. The cell wall substance of the plant is not hydrolysable by the enzymic apparatus of the fungus. As the best evidence available indicates that the protoplast-destroying agent only functions after previous attack on the cell wall by the enzyme—if in fact the two substances are not the same—there is likewise no attack on the living cells. Immunity thus ultimately rests upon the composition of the cell wall. The chemistry of cellulose, hemicellulose, pectin and such like substances is therefore of the very greatest interest to the student of disease resistance.

Reviewing the enzymic theory of parasitism, as applicable at the moment to the facultative type of parasite, one must confess that it is somewhat complex. The excretion of enzyme varies, quantitatively and qualitatively, according to the nutrient conditions prevailing, and even if these are such as to allow of the process, the enzyme may be prevented from working by forces exerted by the living host cells. There is room here for a considerable interplay of factors, and it is just this complexity of action which makes the enzyme theory a promising one. Any theory that aims at some measure of generality must explain why a particular plant, though containing food substances perfectly adequate for the growth of a multitude of cultivable

fungi, is nevertheless parasitised by only very few. It must also explain the more delicate problem of environmental effect on parasitism, viz. that under one set of conditions attack progresses, and under another is stopped. From the point of view of the fungus it must explain why one fungus is able to attack and another not. It must, at one and the same time, be capable of explaining enough but not too much. With these requirements it is plain that a theory resting simply upon the presence or absence of a toxin, either in the parasite or the host, would not lead very far. It is much more likely that fungi as a class have essentially the same mechanism of attack, but that the parasitic vigour shown on any particular plant is determined by quantitative considerations.

In discussing the enzymic theory I have indicated certain features of the mode of action because there is some experimental evidence for the same. The evidence is as yet very fragmentary and it is more than probable that, apart from criticisms which anyone else may offer, I shall see fit to modify some of the views expressed in the light of further work. I set out, however, not merely to review the present state of knowledge on the subject of disease resistance, but to indicate in what directions research could be directed. The latter purpose could not be achieved without some lapses into speculation. This address will have served its purpose if it has shown that there is still a very wide and practicable field of academic study to be explored in the physiology of parasitism.

ISARIA

By T. PETCH

The name *Isaria* was first used by Hill in his *History of Plants* (1751), p. 66. The relevant passages of his account are quoted below, references to male and female flowers being omitted.

"*Isaria* is a genus of Fungi, consisting of stalks of a simple or ramose figure, formed of a circular series of fibres, arranged round a cavernous axis, and each fibre having at it's end a capsule.... The *Isariae* are all very small plants, and the surface of them all is alike of a beautiful granulated structure, it being all composed of globular bodies, applied as closely as possible to one another.

"Micheli met with two species of this genus, which he very justly distinguished from all other fungi, under the name *Puccinia*... We have called the genus, *Isaria*. From the Greek, ἴς, a fibre, these being the only known fungi that are composed wholly of fibres, supporting the fructifications."

Hill's conception of *Isaria*, as is evident from Micheli's figures, is a fungus with a hollow clava, which bears spores at the ends of threads which are perpendicular to the clava. In transverse section of the clava, Micheli showed the "threads" of *Puccinia* as radial. Hill took over Micheli's genus and changed the name; and as far as Hill knew, *Isaria* Hill is a synonym of *Puccinia* Micheli.

Hill's first species was his own "*Isaria ramosa varie divisa*. The variously, divided, ramose *Isaria*," which he described as follows:

"This is an extreamly beautiful little plant. It rises with a single stem rounded, and of the thickness of a small packthread; this runs up single to about a third of it's height, and from thence begins to divide into a number of lesser branches: these ramify again, and at length the whole forms a kind of little bush with the branches, all erect, and terminating in obtuse points. The whole plant is of a deep orange colour, and it's height is more than half an inch. The surface of the branches, when examined with a microscope, appear beautifully and regularly granulated: when cut transversely, and examined, they are found to consist of a cylindric, cavernous core, around which are ranged series of fibres very short and slender, each, at it's extremity, supporting an oval body....

"This beautiful fungus is common in Charlton Forest in Sussex, growing to the decaying bodies of beeches and other trees. I never saw it elsewhere, nor has any author described it."

Hill also included in his genus two species which he took from Micheli, *Nova Plantarum Genera*, viz. *Isaria simplex*, which was Micheli's *Puccinia non ramosa major pyramidata* (Micheli, tab. 92, fig. 1), and

Isaria ramosa bifida, which was Micheli's *Puccinia ramosa, bifurcata omnium minima* (Micheli, tab. 92, fig. 2).

Micheli's species are known. The first is a *Gymnosporangium*, and the second a Myxomycete, *Ceratiomyxa fruticulosa*. But the type species of Hill's genus, according to modern views, is his *Isaria ramosa varie divisa*, and no one appears to have made any attempt to identify it. The only solution which suggests itself after reading his description is that it was *Calocera viscosa*. In any case, Hill's conception of *Isaria* is widely removed from that of the present day.

Linnaeus, *Systema Naturae*, Ed. 13 (1791) by Gmelin, did not include *Isaria*.

Persoon, *Dispositio Methodica Fungorum* (1794), included *Isaria*, with the generic description, "*Erecta subramosa, pilis densis laevibus pulverulentis obsita*," and two species, *Isaria mucida* and *Isaria agaricina*. The first of these is again *Ceratiomyxa fruticulosa*, while the second is *Isaria brachiata* (Batsch) Schum. Persoon did not refer to Hill, but there is no doubt that he took the name *Isaria* from him. He returned Hill's second species to Micheli's genus *Puccinia*, and retained the third species in *Isaria*. Evidently he could make nothing of the "type species."

The *Dispositio* was republished in 1797, as *Tentamen dispositionis*, etc., with a supplement in which Persoon extended his definition of *Isaria* to "*Erecta simplex furcatimque divisa, pulvere farinaceo aut pilis densis obsita.*"

Meanwhile, Persoon had written his *Commentatio de Fungis Clavaeformibus*, which was also published in 1797. In this he gave the generic description of *Isaria* as "*Byssoidea simplex ramosaque, pulvere farinaceo utplurimum obtecta.*" The first species mentioned was *Isaria crassa* Pers., which is usually taken to be one of the forms of *Isaria farinosa*. He still, however, retained *Isaria mucida* in the genus.

In Persoon, *Synopsis Methodica Fungorum* (1801), the generic description of *Isaria* is "*Subbyssoidea, simplex ramosaque, pulvere farinaceo (subfilato) obtecta. (Substantia molliuscula. Color albus).*" The type species is again *Isaria crassa*, *Isaria mucida* being the third in the list and *Isaria agaricina* the fourth.

In 1805, Albertini and Schweinitz (*Conspectus Fungorum*) instituted a new genus, *Ceratium*, for *Isaria mucida* Pers., and enumerated *Isaria*, without any generic description, with *Isaria crassa* as the first species. As they cited only Persoon, *Synopsis*, in this connection, they would probably have been unaware that they were transferring the original type species of Persoon's genus, even if the idea of type species had ever occurred to them.

Link, *Observationes* (1809), described *Isaria* as "*Stroma elongatum, simplex, clavatum, aut ramosum, carnosum lignosumque, floccis tectum simplicibus ramosisve. Sporidia floccis inspersa*," and added the species, *Isaria velutipes* Link, which is now taken to be one of the forms of *Isaria farinosa*.

Nees, in *System der Pilze* (1817), gave a long account of the genus *Isaria*, and placed as his first species, *Isaria bulbosa* Nees. His account of the genus shows that he had the modern idea of it, but his species has never been identified again. Link (*Species Plantarum*) suggested in 1825 that it was a juvenile condition of *Isaria glauca*; and Lindau (*Rabenh. Krypt.-Fl.*) stated that the description was so indefinite that it had better be discarded.

Persoon, in *Mycologia Europaea* (1822), accepted the genus *Ceratium* A. & S. He again altered the generic description of *Isaria* to "*Elongata, subclavaeformis, simplex ramosaque, sicca, floccoso-furfuracea. (Color plerumque albus).*" His first species was now *Isaria truncata*, which had been placed second to *Isaria crassa* in *Synopsis Methodica Fungorum*, but as these are regarded as synonymous the change is immaterial.

In *Species Plantarum*, Ed. 4 (1825), Link altered his generic description to "*Thallus dense contextus. Sporodochium elongatum simplex aut ramosum, superne floccosum. Sporidia floccis inspersa,*" and added the note "*Sporidia globosa semper minuta.*" He placed first, *Isaria crassa* Pers., with *I. truncata* Pers. and *I. velutipes* Link as synonyms.

Fries, in *Systema Orbis Vegetabilis* (1825), included "*Isaria* Pers. *Receptaculum elongatum, continuum, simplex aut ramosum, siccum, persistens, floccis obductum. Sporidia globosa, floccis inspersa. Coloratae, saepius albae,*" but cited Nees, *Syst.*, p. 85. In *Systema Mycologicum III* (1832), he wrote "*Isaria* Hill *ex em. Receptaculum elongatum, contiguum, e floccis dense intricatis coalitum. Flocci sporidiiferi investientes, patentes. Sporidia globosa, simplicia, inspersa.*"

Persoon (except in the *Dispositio*) and Link had emphasised the entomogenous nature of some of the Isariae by placing the entomogenous species first in the genus. Fries, however, discarded that arrangement and placed first the species which grew on the ground and on dung, beginning with *Isaria terrestris* Fries, which he stated was not indeed one of the largest species, but was pre-eminently typical and distinct.

Saccardo, in *Michelia II*, 32 (1880) cited *Isaria* Hill, with the type species, *Isaria farinosa* Fr. In *Sylloge Fungorum IV* (1884), he cited *Isaria* Pers., *Tentamen*, with the same type species.

Lindau (*Rabenh. Krypt.-Fl. IX*) also cited *Isaria* Pers., *Tentamen*, but placed as his first species *Isaria intricata* Fr.

Isaria Hill is, by intention and as far as can be definitely determined, a synonym of *Puccinia* Micheli. Hence, if the rule "Once a synonym always a synonym" is adhered to, the name *Isaria* cannot be used again.

Isaria Persoon, *Dispositio* (1794) and *Tentamen* (1797) is, by the method of type species, a Myxomycete.

Isaria Persoon, *Commentatio* (1797), *Synopsis* (1801), *Mycologia Europaea* (1822), and *Isaria* Link, *Species Plantarum* (1825), is a fasciculate or concrescent *Spicaria*.

Isaria Nees, *System der Pilze* (1817), is indeterminable.

Isaria Saccardo, *Michelia* (1880) and *Sylloge Fungorum* (1884), is a fasciculate or concrescent *Spicaria*, as far as regards the type species, but it is not *Isaria* Hill (1751) nor *Isaria* Persoon, *Tentamen* (1797).

Isaria Lindau (1908) is again not *Isaria* Persoon, *Tentamen* (1797), nor is it equivalent to any other author's *Isaria*, since *Isaria intricata* Fries is not a fasciculate *Spicaria*. It might, however, be argued that *Isaria* Lindau is equivalent to *Isaria* Persoon, *Tentamen*, *emend.* A. & S., since the removal of *Isaria mucida* left only *Isaria agaricina*, which is co-generic with *Isaria intricata* Fr. But Albertini and Schweinitz dismembered *Isaria* Persoon, *Synopsis*, not *Isaria* Persoon, *Tentamen*.

Isaria Fries, *Systema Mycologicum* (1832), has for its type species *Isaria terrestris* Fr., which was described as "*Simplex, aequalis, basi villosa nigrescens, apice dilatata truncata alba, floccis sporidiiferis vestita*," with a further long explanatory note. It was collected in Sweden, on bare ground on hill sides in beech woods, and does not appear to have been recorded since. By the courtesy of the officers in charge of Fries's herbarium, I have been furnished with a slide made from the type specimen.

The synnemata either arise from a brown conical base, or several strands, up to 0·15 mm. broad and composed of parallel brown hyphae, arise separately from the substratum and converge, uniting at a height of about 1 mm. to form the synnema. The latter is about 3 mm. high, with a brown central column of parallel hyphae, up to 0·4 mm. diameter, surrounded by a weft, up to 0·25 mm. thick, of loosely interwoven, contorted, thick-walled, brownish hyaline hyphae. Towards the apex the colour becomes brownish white, the synnema expands, and the apex is abruptly truncate, the synnema growing out in a flat expansion perpendicular to the axis of the column, on one side only (in my specimens). On the upper surface of this expansion the hyphae are regular, in continuation of the regular hyphae of the central column; on the lower surface, they are irregularly contorted and interwoven, like those of the exterior of the column. There are no conidiophores or conidia. On a few free brown hyphae which run into the bases of the synnemata, clamp connections are present, but it is doubtful whether these hyphae are those of the *Isaria*.

There would appear to be two possible explanations of the truncate apex—one, that the synnemata encountered some obstacle which changed their direction of growth; the other, that the fungus is a developing Hymenomycete, and that, as in *Septobasidium*, the lateral growths from the apices of the synnemata would fuse with one another and produce a hymenium. There is nothing in the specimen to show that it is a Hyphomycete.* It would appear to be more probably the initial stage of a Hymenomycete. But the question can be decided only by finding it again in the type locality and watching its development.

Thus, Fries's type specimen is indeterminable, and consequently we cannot cite *Isaria* Fries (1832). To retain the name *Isaria* for a genus of Mucedinaceae, we must cite *Isaria* Persoon, *Commentatio* (1797) or *Synopsis* (1801), with the type species, *Isaria farinosa* (Dicks.) Fr., of which *Isaria crassa* Pers. and *Isaria truncata* Pers. are synonyms.

There is another, and more important, aspect of the question, what is *Isaria*. The prevailing idea of the genus since the time of Persoon has been an erect fascicle of mucedinous, amerosporous conidiophores united, in part, into a stalk or clava of varying height. Many species included in *Isaria* do not agree with that conception, but have been placed in the genus merely because they grew on insects. That was perceived by Persoon, who adopted the genus *Ceratonema* for *Isaria sphecophila* Ditm. But, excluding such obvious misfits, the genus has been a centre for species which agree only in their most general shape. It is a form genus in the widest sense of the term, more general than *Agaricus* when used for all lamelliferous Hymenomycetaceae, and almost as unscientific as *Clavaria* in the sense of Holmskiold.

The unsatisfactory nature of the genus was evident to Fries, who remarked that it embraced species which differed from one another in structure and in the mode of origin of their spores. It would appear that the type of conidiophore is of greater importance in classification than the fact that the conidiophores are united. In identifying an *Isaria*, the type of conidiophore should be the primary diagnostic character, and it is almost impossible to interpret the descriptions of very many species of *Isaria*, because the type of conidiophore has not been recorded.

Presuming that the genus *Isaria* is retained, with *Isaria farinosa* as the type species, then *Isaria* is a compound *Spicaria*. Species which have a different type of conidiophore cannot remain in the genus, and a large number of other genera will have to be instituted for them. That, indeed, will happen, whatever species is taken as the type. But the isarioid form is not necessarily an invariable feature of a species. *Isaria farinosa*, for example, frequently occurs as a simple *Spicaria*, and conversely, *Beauveria densa* may take the isarioid form. Nor have all isarioid species been consistently placed in *Isaria*; *Botrytis Tilletii*, for example, is an *Isaria* in the wide sense in which the name has hitherto been used.

It would seem simpler to discard the genus *Isaria*, and to distribute the species among the corresponding mucedineous genera. In most species, the type of conidiophore agrees with one of the established genera of Mucedinaceae. The name *Isaria* might be retained as a descriptive term, parallel to sporodochium and synnema, or it might be used to distinguish the isarioid species of a genus, e.g. *Spicaria* (*Isaria*) *farinosa*.

AN EVOLUTIONARY STUDY IN AGARICS: *COLLYBIA APALOSARCA* AND THE VEILS

By E. J. H. CORNER, M.A.
Botanic Gardens, Singapore

(With 13 Text-figures)

A problem which must be solved before the evolution of agarics can be understood is the nature of the veils. They are considered advanced features and genera are based on the degree of their development. Primitive genera, as *Clitocybe* and *Paxillus*, have no veils; others, such as *Tricholoma* and *Hebeloma*, have a thin universal veil, which is thicker and developed to a marginal veil in *Armillaria* or *Pholiota*; in the most advanced, as *Amanita*, there are universal, marginal and partial veils. But in many genera, such as *Naucoria* and *Boletus*, these distinctions are merely sectional and, more perplexing still, in several groups of common and by no means primitive agarics they are specific or even subspecific. For instance, both *Armillaria mucida* (Schrad.) Fr. and *A. mellea* (Vahl) Fr. have a thick universal veil leaving a ring on the stem, and *Collybia radicata* (Relh.) Berk. and *Clitocybe tabescens* Scop. are gymnocarpic without a veil: yet *Collybia radicata* is closely allied to *Armillaria mucida*, and *Clitocybe tabescens* differs in no other respect from *Armillaria mellea*. Further, *Amanita gemmata* Fr.(12) has two forms equally abundant, one, *Amanitopsis adnata* (W.G.Sm.), Sacc. with a universal veil and volva, and the other, *Amanita junquillea* Quél., with a partial veil and ring in addition. Clearly the evolution of the veils has been polyphyletic and homoplastic, and each species needs separate investigation.

I have been enabled to approach the problem in the *Collybia radicata—Armillaria mucida* group by an investigation of *Collybia apalosarca* B. & Br., which is intermediate in many respects, structural and biological, between the two and it has a rudimentary veil. I have examined the structure of the mature fruit body of the Malayan form of *C. radicata*, though I have been unable to work out the development—even to find young ones—on account of its sporadic and solitary mode of growth in this country. Fischer's morphological description of *Armillaria mucida* is brief, and as the species is a temperate one it was not available for study in Malaya.

Collybia apalosarca is common in the eastern tropics, and has received many names. It was placed in *Pluteus* and *Phaeolimacium* by Hennings and in *Oudemansiella* by v. Hoehnel, in which respect he is followed by Petch(19), but it is preferable in our present knowledge of generic

limits in Basidiomycetes to conform with the straightforward Friesian classification and to retain the original combination. As Petch has dealt in full with the history and synonymy of the species, it need not be recounted save to remark that *Mucidula alphitophylla* (B. & Curt.) Pat., from the description, is certainly the same. I identified the Malayan material from Petch's description; that which is given here is based on the Malayan material which differs in no essential.

In Malaya *Collybia apalosarca* occurs on dead wood in the lowland forest, though it may be found in estates and gardens in very wet weather. It is particularly abundant in the rainy season in forest reserves where the second class trees have been ringed and left to die; tufts of fruit bodies then develop on the dead standing trunks at all heights up to 50 ft. from the ground, and from a distance they have very much the appearance of the "beech-tuft." It does not grow from underground wood and is never terrestrial as *C. radicata*. It is probably abundant in the mountains also, since I found it frequently at 4000 ft. on Fraser's Hill, Pahang, and at a similar elevation at Brastagi in Sumatra: it is odd, therefore, that it has not been reported from south temperate countries.

The material for the developmental study came from a felled trunk of *Araucaria* on Government Hill in Singapore. A large section, 3 ft. long by 1 ft. thick, was brought to the Botanic Gardens, stood in a shady place and well watered every day: it is now two years since the study began and the log still bears abundant fruit bodies in wet weather. Petch considers that *C. apalosarca* may be parasitic, but I have seen no evidence of this in Malaya, and from Fischer's work it is doubtful even if *Armillaria mucida* is a true parasite.

The material of *Collybia radicata* was gathered scantily in Singapore and Pahang, and at Brastagi in Sumatra. It occurs in the lowland and mountain forest but is rather scarce, and the fruit bodies never form troops on cut stumps as in Europe; they grow singly, or two or three together, from dead roots and appear to be humicolous.

Description

Collybia apalosarca B. & Br.

Pileus 4 mm.–15 cm. wide, convex then *plane*, often gibbous, never revolute, sometimes rugulose, *with a smeary viscid gelatinous pellicle* often spotted with greyish flecks, striate in small specimens, *dark umber becoming paler fuscous brown and finally dirty white when old*, rarely pallid white from the first; margin slightly incurved at first, thin, acute, entire.

Stem 3 mm.–9 cm. long by 0·5–9 mm. wide at the apex, 1–14 mm. at the base, gradually tapered upward or subcylindric, central or

slightly excentric, straight or incurved; *base dilated, discoid, mostly with a narrow ridge or zone round the distal margin as the trace of the ring*; solid, fibrous; attached by a microscopic root; *thinly white villous below the ring*; *above the ring, pruinose or subvillous, white or pale clear yellow when young*, sometimes with pale rufescent streaks; apex often subcostate.

Veil very thin, evanescent.

Gills rounded adnate, adnexed or almost free, often separating free, sometimes with a subdecurrent tooth, more or less ventricose, *rather crowded, broad, rather thick, waxy*, submucilaginous, not veined, 1–5 ranks with 11–39 primaries, 1–12 mm. wide, *white, often with the edge pale clear yellow at first*, becoming powdered with the spores and brownish in decay.

Flesh fairly thick, subhygrophanous, rather brittle, 0·5–5 mm. thick in the centre, 0·3–3 mm. thick half-way to the margin, *white, with a thick gelatinous layer*, 0·3–1 mm. thick *on the surface of the unexpanded pileus.*

Smell of fresh fish, sometimes strong.

Spores 16–23 × 16–22 μ, white, *subglobose* to broadly ellipsoid, with a small apiculus, *smooth*, with the wall thickened about 0·5 μ, *densely granular-guttulate* with fine oil-drops.

Basidia 54–75 × 18–25 μ, *large*, subclavate, monomorphic, *densely multiguttulate* as the spores, with four stout subarcuate sterigmata 5–9 μ long × 3·5–5 μ wide at the base.

Cheilocystidia forming a sterile edge to the gill, *clavate*, rarely subventricose, often with a long stalk thin-walled, colourless, vacuolate, 45–95 × 8–28 μ, mostly 10–15 μ, and 2·5–4 μ at the base.

Pleurocystidia 110μ–280 × 23–40 μ in the middle, 10–16 μ at the apex and 3–4·5 μ at the base, *very large, broadly fusiform* with rounded apex *or ventricose* with the apex prolonged and subcylindric, with a long thin stalk, colourless, vacuolate, thin-walled.

f. **radicans** f.nov.

Stipes radicans, e rhizomorpho longo evolutus.

A modification with a "rooting base"; common with the typical form.

var. **perstipitata** var.nov.

Stipes ex integro elongatus, velo universali a basi usque ad medium tenuiter tunicatus disco basali deficiente.

The stem elongating from the base, without a disc, thinly sheathed with the veil which ends in an indistinct zone about the middle; of small size, the pileus not exceeding 5 cm. wide and the stem 6 cm. long. Much less common than the typical form.

The structure of the mature fruit body

The microscopic structure is complicated. Almost every apical cell on cessation of growth enlarges into a basidium or a cystidium, these varying in size and shape in different parts of the fruit body, and forming a palisade at every external and internal surface. Fig. 1 is a diagram of the structure of a primordium in which the marginal

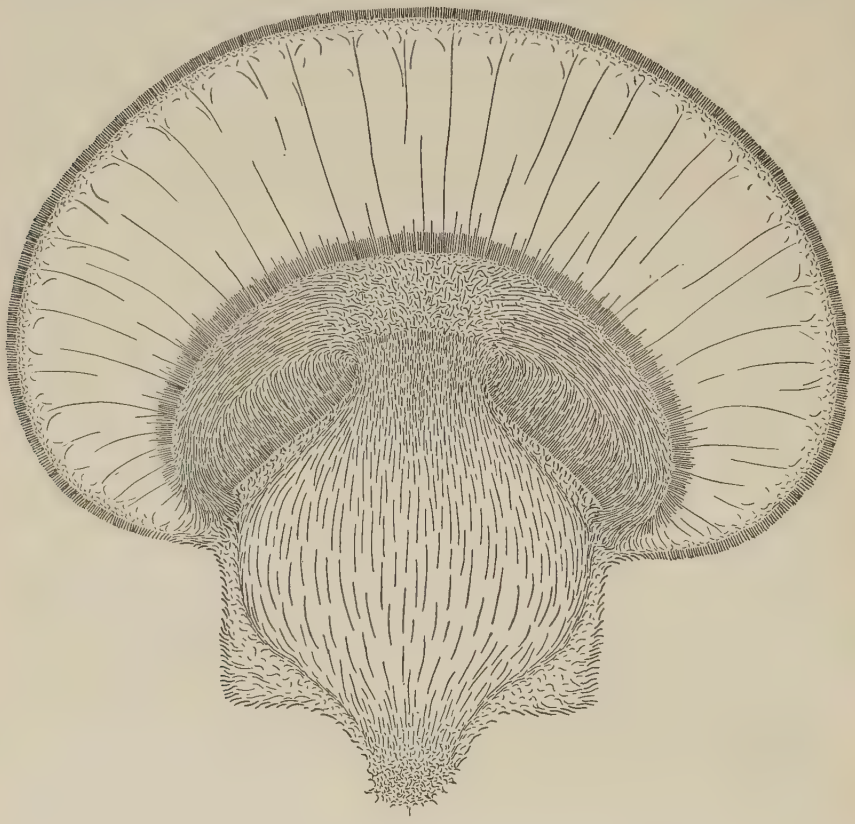

Fig. 1. A diagram of the structure of a primordium about 6 mm. high, in which apical growth of the parts has finished.

growth of the pileus and the down-growth of the gills have been completed: all parts of the fruit body are thus defined and need but to expand by sympodial branching and inflation of the cells to their full size. Immediately above the point of emergence of the stem from the wood there is a bulbous base which will become the disc. The shank of the stem is confined in a short, rapidly tapering frustrum of a cone and is surrounded by the pileus, whose margin is attached by the

veil to the edge of the disc. A thick gelatinous blanket envelopes the pileus. The gills almost fully occupy the gill cavity.

A loose palisade forms a thin villous layer round the sides of the disc. It is continuous with the *external* palisade of the pileus, which together with its thin interwoven hypoderm forms a superficial elastic pellicle holding the jelly in place. Another loose palisade covers the supra-annular portion of the stem. Along the edges of the gills and at the margin of the pileus there is a close palisade of sterile cells which differ in shape from the cystidia in the hymenium, and at the boundary between the jelly and the firm flesh of the pileus there is the *internal* palisade of the pileus.

For convenience in description, I have followed Buller's method of naming the sterile apical cells of the fruit body (6). Those on the surface of the pileus are *pileocystidia*, those on the stem are *caulocystidia*, those on the sides of the gills are *pleurocystidia* and those on the gill edges are *cheilocystidia*.

The detailed structure of the parts is as follows:

The stem. The medullary hyphae in the elongating part of the stem are colourless, thin-walled, strictly longitudinal and compact. In the middle portion, between the disc and the stem apex, the cells are 100–800 × 8–30 μ, mostly 12–20 μ, but a few are uninflated, only 3–5 μ wide, and are passively drawn out to various lengths. At the apex of the stem the cells are as wide but shorter, 50–200 μ long. At the base of the stem and in the disc they are 5–12 μ wide and too much interwoven for their lengths to be measured. In the plug, which fixes the fruit body to the wood, the hyphae are not inflated; they are 3–5 μ wide, very closely interwoven, without air spaces between them, and with firm, slightly thickened walls; they thus form a strong tough rope-like tissue.

The palisade on the disc is composed of thin-walled, colourless hyphae, 3–5 μ wide, loosely interwoven and directed obliquely outwards. Their terminal cells are slightly inflated, 5–8 μ wide, and subclavate or subventricose, with clear vacuolate contents; the walls may be smooth or thinly encrusted in places with minute yellowish granules.

The outer medullary hyphae in the supra-annular portion are narrow, 2–6 μ wide, and bear superficial branches which project more or less obliquely outwards to form the loose palisade, macroscopically the pruinosity. This palisade is best developed in the proximal half of the stem and is absent from the extreme apex, which macroscopically is glabrous. The palisade is formed from laterals which grow out into the gill cavity in the primordium; at the apex the gills are pressed so tightly against the stem that not a single cell can be extruded. In the proximal half, the hyphae of the palisade are composed of two or three cells, each 40–90 μ long, and the palisade is rather denser than on the disc. Towards the apex of the stem, the

hyphae are shorter and reduced to single cells. The terminal cells are inflated, 6–17 μ wide, and are ventricose, subfusiform or clavate, thin-walled and colourless; their contents are either widely vacuolate or rather vitreous and smeary-looking with few vacuoles, or wholly clouded with very fine vacuoles and minutely reticulate. The subterminal cells are either cylindric, 3–5 μ wide, or also more or less swollen, up to 15 μ wide, and with similar contents. On the elongation of the stem the palisade is more or less disrupted and the pruinosity may tend to become a minute scurfiness.

Fig. 2. A part of the palisade from the middle of the stem of *Collybia apalosarca*: × 500.

Among these superficial hyphae are numerous yellowish, oily-looking blobs and granular masses which may be derived from the breakdown of some of the hyphae, or may be exudates. When abundant they cause the clear yellowish tinge often seen on the stem of fresh specimens. They sometimes occur on the gill edges and impart to them the same colour.

A secondary mycelium is absent.

The pileus. The hyphae are interwoven in the centre, immediately above the stem, and longitudinal in the limb. They have thin colourless walls and are widely vacuolate. The cells are 60–500 × 8–30 μ, though a few may be narrow, 3–5 μ, and passively drawn out as in the

stem. Air spaces occur between the hyphae, which have dry walls, except over the gills and in the trama, where the spaces between the hyphae are reduced and filled apparently with free water.

The internal palisade is formed of narrow hyphae directed perpendicularly into the jelly from the surface of the pileus, as shown in Fig. 3. It is about 100 μ high. The hyphae are 2–3·5 μ wide, in places swollen to 6 μ; they have short cells, 25–50 μ long, which are

Fig. 3. A part of the internal palisade from the centre of the pileus of *Collybia apalosarca*: × 500.

frequently branched, one to four branches arising near the distal end of each, and they terminate in simply rounded apices. Their cell contents are vacuolate with a pale fuscous or pale umber pigment in the cell sap.

Immediately below the internal palisade there is a narrow hypoderm, 30–40 μ thick, of rather closely interwoven, narrow hyphae, 2–5 μ wide, also with the pale umber pigment in the cell sap. It is these hyphae which have given rise to the palisade and they are intricately entangled, becoming stretched and distorted when the pileus expands.

The jelly is traversed perpendicularly to the surface of the pileus, by rather scattered, fine, colourless hyphae, 1·5–2·5 μ wide, the cells of which are 50–150 μ long and have tenuous mucilaginous walls. They issue from the flesh of the pileus; most of them pass through to the external palisade, forming tufts of pileocystidia, but others end

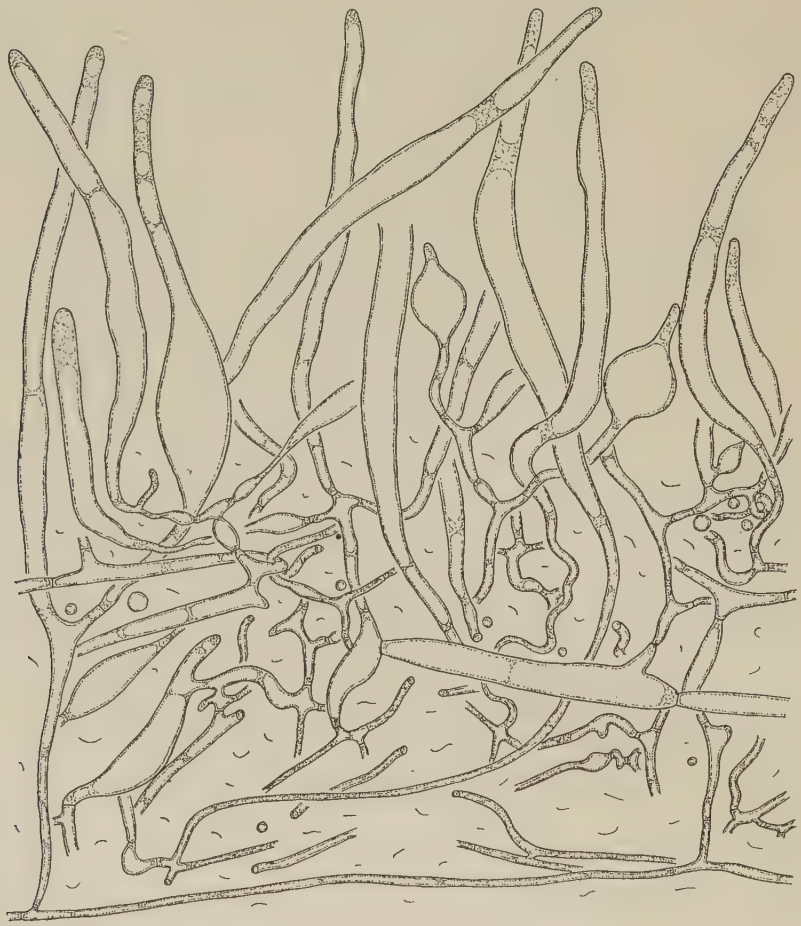

Fig. 4. A part of the external palisade from the centre of the pileus of *Collybia apalosarca*: × 500.

blindly in the jelly and represent hyphae of the internal palisade which have grown out beyond the general level. The thickness of the jelly varies with the amount of water available; in wet weather, it may reach 2·5 mm. thick in the primordium. On expansion of the pileus it is stretched and slithers off, and in dry weather it is thin and rubbery.

The external palisade is formed from the terminal cells of the hyphae which traverse the jelly (Fig. 4). These pileocystidia are very variable in shape and size. They are ventricose, flask-shaped or subcylindric, rarely clavate, often flexuous, 70–200 × 6–11 μ, with vacuolate contents and mostly with the pale umber pigment in the cell sap. Beneath the palisade there is a hypoderm of rather closely interwoven hyphae which have arisen as branches from the subterminal cells, and their terminal cells contribute also to the palisade: the cells of this layer are mostly 35–200 μ × 2–5 μ but they may be inflated up to 12 μ wide, and, as in the hypoderm of the internal palisade, they are pulled out and distorted on expansion of the pileus. The palisade is at first fairly compact, but, as the primordium enlarges, it is stretched also and the pileocystidia are pulled apart and come to lie in any direction; finally, on full expansion, the pellicle is torn into small pieces which persist as grey flecks or are washed off by the rain.

The gills. The trama is composed of longitudinal, fairly compact hyphae similar to those of the pileus. (By longitudinal in the gills is meant in the direction of marginal growth, which is normal to the limb of the pileus.) The hyphae in the subhymenium are closely and intricately interwoven: they have slightly mucilaginous walls and their cells are short and narrow, 10–25 × 3–6 μ, though occasionally 12 μ wide.

All the hyphae of the fruit body have a clamp at each septum except those of the internal and external palisades with their hypoderms and those which traverse the jelly; they are not clamped.

The macroscopic development of the fruit body

I observed carefully the development of fifty-one fruit bodies. For twenty-one of these I was able to record the rate of growth from the first white flecks visible to the naked eye to the collapse and decay: for the rest, the observations cover only the later stages from expansion to collapse.

On the large log of *Araucaria*, fruit bodies of all sizes developed, from those with mature pilei only 4 mm. wide to others with the pilei 14 cm. wide: but from smaller bits of wood, 8–12 in. long × 3–4 in. thick and wide, and on bits of bark, only small fruit bodies were obtained, none of which had pilei larger than 5 cm. wide. For the production of large fruit bodies it thus appears that the mycelium requires a large piece of wood to grow in.

The primordia are mostly solitary. When two or three are formed close together one usually takes the lead at an early stage and the others abort or develop into stunted specimens. Once, however, a tuft of six almost equally developed fruit bodies with pilei 6 cm. wide was produced from the large log, and tufts of three to five large indi-

viduals are occasionally found in the forest. Sometimes also, for no apparent reason, the primordia develop normally for two to three days, then stop, shrivel and rot away: a great many of my observations were nullified in this way.

When the hyphae grow out from the bare wood or from the surface of bark, they develop straightway into the primordium which is thus attached only by a microscopic "plug" to the mycelium. But if they arise under the bark or in a deep crack, they then grow out into a long cylindrical or flattened white strand, 1–2 mm. thick. While it is confined the apex of the strand is conical, but on reaching an opening, or on being acted upon by light of sufficient intensity, it dilates into the primordium. Such fruit bodies have thus a distinct "root" of varying length. The "root" is homologous with that of *Collybia radicata*. It should be regarded as a short rhizomorph.

For convenience, the fruit bodies which I studied can be divided into four groups, namely large ones with the mature pileus 6–11 cm. wide, medium-sized ones with the pileus 2–5 cm. wide, small ones with the pileus less than 2 cm. wide, and perstipitate ones in which the pileus did not exceed 4 cm. wide. Most observations were made on medium-sized ones. The primordia were always superficial and development was straightforward.

The primordia are first visible as minute white flecks about 100 μ high, which can scarcely be more than a few hours old; they develop at any time of the day. In twenty-four hours they are about 1 mm. high and the pileus has just begun to form. The apex of the primordium is rounded and slightly greyish, since the hyphae of the veil above the pileus have already begun to gelatinise. During the next fifty hours or so, the primordium gradually develops into a sessile, or shortly stalked, dark brown hemispherical body about 6 mm. high. In this state it corresponds in structure with the diagram in Fig. 1: the tissues of the stem, pileus and gills are completed, and on inflation of the cells and development of the spores the fruit body will become mature. The brown colour of the upper surface begins to develop when the primordium is only thirty-six hours old, and it is due to the appearance of the pale umber pigment in the palisades of the pileus. The rest of the primordium is seen in section to be white, though sometimes the surface of the stem and the edges of the gills are yellow from the granular matter deposited on them.

Having developed thus far, the primordium expands on the following night and by next morning the pileus is about half-open. It remains like this during the daytime and on the next night it expands fully, the limb becoming plane. The fruit body then persists in this state for another thirty-six hours or so. On the first night, expansion does not begin until after dusk and is probably not appreciable before 9–10 p.m. Elongation begins in the stem just above the disc and pro-

ceeds thence acropetally to the apex and centrifugally along the limb and down the gills. The limb rises both through the inflation and straightening of its own hyphae and through the upthrust of the gills. And if, as usually happens, the primordium has developed from an oblique or vertical surface, it is during this first night of expansion that the pileus is set so that the longitudinal axes of the gills are brought vertical and both sides of the gill face obliquely downwards. The adjustment is brought about by a curvature of the stem apex, the cells on the under side elongating more than those on the upper side: for, it will be remembered, the cells in this part are not fully extended and thus have a reserve to effect such alterations.

The veil is ruptured during the first night in the early hours of the morning; as the hyphae in the stem and the centre of the pileus elongate, the limb is forced upward and outward and the margin breaks away from the disc leaving the narrow ridge round its margin as the trace of the ring (inferior annulus). The grey pellicle on the pileus is split up into irregular patches and the jelly, thus freed, slithers over the surface and drips from the edge or, if the veil clings more firmly on one side of the disc, the jelly is drawn over from the opposite edge of the pileus and collects in a sloppy mass round the stem.

The first spores are shed a little before the rupture of the veil so that they are not properly dispersed. In a few hours, by sunrise, sporing is copious and lasts until the collapse of the fruit body.

The gills generally collapse first owing to the numbers of bacteria which develop among the effete basidia. Then the pileus follows in a few hours, hanging limply round the stem. But the base of the stem and the disc are firmer, their hyphae having slightly thickened walls, and they persist as unsightly relics for several days. The hyphae can maintain their turgidity only for a few days.

The primordia are not attacked by beetles, but small flies lay their eggs on the gills and their minute maggots browse on the hymenium, just as in *Collybia radicata*. Snails devour the fruit bodies at any stage and special measures had to be taken against them.

So, of the six and a half days which are the span of life of a medium-sized fruit body, three and a half are spent in developing a hemispherical primordium. Expansion is accomplished in the ensuing twelve hours of darkness on the fourth night and sporing lasts for a little over two days.

The procedure in small fruit bodies is almost the same. The development of the primordium takes some twelve hours less, but they expand on the fourth night. The pileus is always fully open by the next morning, and thus the fruit body lasts longer, for about fifty hours, in the mature state.

The primordia of large fruit bodies take nearly a whole extra day in

developing, thus reaching a larger size, and they do not expand until the fifth night. As with the medium-sized fruit bodies, the pileus is only half-open on the next morning and flattens out on the following night. The fruit body also lasts for a third day after expansion and persists in the mature state for about sixty hours. The span of life of large fruit bodies is therefore eight and a half days and they spore for a little over three days.

The development of the perstipitate variety is intermediate in character. It also does not expand until the fifth night, taking four to four and a half days for the development of the primordium, but it lasts only for two days after expansion like the medium-sized fruit bodies. The pileus may be fully open by the morning following expansion, as with small fruit bodies, or not until the second morning as with medium-sized and large fruit bodies: and this regardless of size. The process of expansion is also rather different, being less confined temporally as well as spatially. The elongation of the stem proceeds acropetally from the very start; the primordium of the pileus is projected farther and farther from the substratum. The part which elongates in this stage is the infra-annular portion of the stem, equivalent to the disc in the typical form, but the parts which elongate on the night of expansion are the supra-annular portion, the pileus and the gills, just as in the typical form. It will be shown presently, that even in the typical form the cells begin to elongate in the stem before the pileus is completed and the resulting increase in height of the primordium accommodates the limb and the gills in their down-growth, but this primordial expansion is macroscopically insignificant compared with that which takes place on the opening of the mechanism.

Perstipitate fruit bodies with relatively slight elongation of the infra-annular portion of the stem are usually as firm and stable on expansion as the typical form, but those with a long infra-annular portion are very insecure, especially when growing from a vertical surface. They have no supporting disc, and as the pileus expands the stem sags lower and lower, necessitating greater and greater curvature of the apex to set the limb and increasing the moment of the pileus about the origin of the stem. Finally, the fruit body usually spins round and hangs upside down in a most impracticable manner. To ensure normal development, I was obliged to prop them up with pieces of wood on the afternoon before expansion.

The data on development are arranged in Table I and schematised in Figs. 5 and 6. The period of development covers the interval from inception of the primordium to the flattening of the pileus; the period of maturity extends from the end of development to the collapse of the fruit body. It must not be supposed that the time intervals will always apply rigidly, but they give a fairly accurate idea of the life of fruit bodies of different sizes. On the whole the larger the fruit body

the longer the periods of development and sporing, but between the largest and the smallest there is little difference. The smallest had a mature pileus only 4 mm. wide and stem 3 mm. long, so that in linear measure it was about one-twentieth of the size of the largest (pileus 11 cm., stem 4·5 cm.) which I observed develop: yet, its period of development was 82 hours, and that of sporing 52 hours, compared with 116 hours and 76 hours respectively for the large one. This small specimen had the shortest life (134 hours) which I observed. But another small specimen (pileus 6 mm.) lasted in the mature state

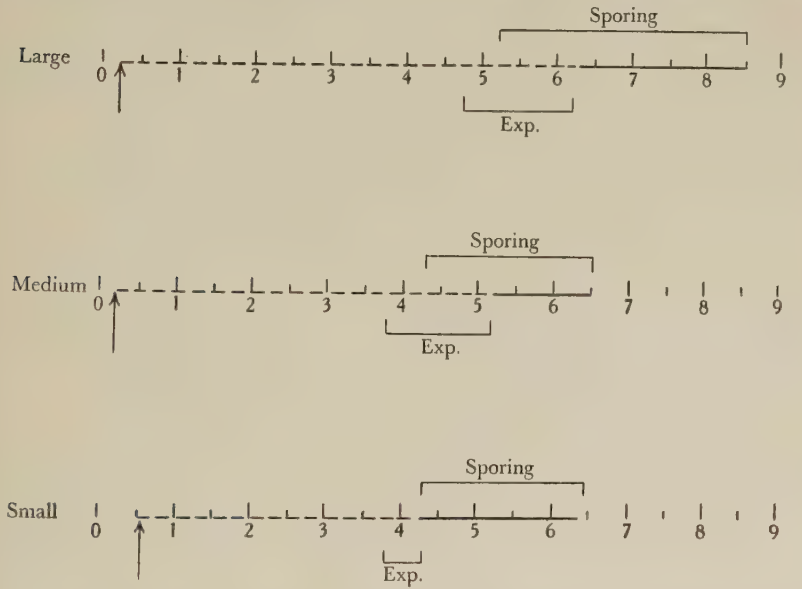

Fig. 5. A scheme of the life histories of large, medium-sized, and small fruit bodies: the periods starting from midnight (0 hours 0 days) at the origin: the figures marking intervals of twenty-four hours (12 a.m. on successive nights) with the points of midday indicated by short vertical dashes: the broken line covering the period of development from inception at the arrow: the continuous line covering the period of maturity: *exp.* the period of expansion.

nearly 60 hours and had a life of 152 hours, which is as long as that of medium-sized fruit bodies. The longest life was that of a large specimen (pileus 8 cm.) which expanded, as usual, on the fifth night but lasted an extra day in the mature state, thus having a life of nine and a half days, a sporing period of four and a half days and a period of maturity of more than three days. The shortest period of sporing (barely 48 hours) and the shortest period of maturity (26 hours) was observed in a medium-sized fruit body (pileus 3 cm.) which was not fully expanded till after the fifth night; it had a life of just over six days.

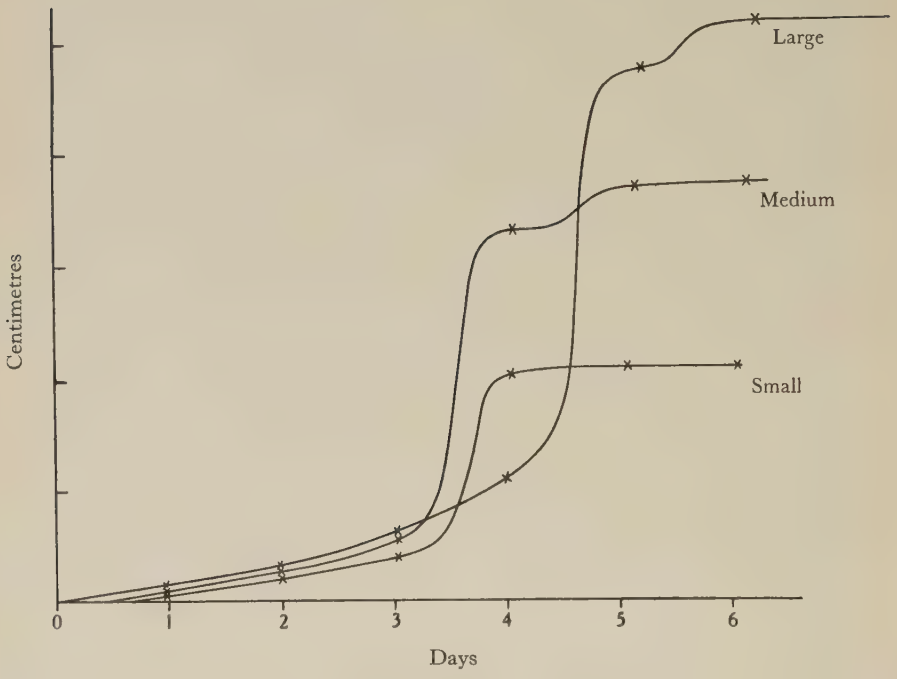

Fig. 6. A graph showing the rate of growth of large, medium-sized, and small fruit bodies: the heights of the fruit body as ordinates, the intervals of time as abscissae: the readings taken at 8 a.m. on successive days.

Table I

	Width of mature pileus	Size of primordium on the afternoon before expansion	Life	Period of development	Time at which expansion begins	Period of sporing	Period of maturity
Large fruit bodies	60–110	12 high × 10 wide	200	140	110th	78	60
Medium-sized fruit bodies	20–50	6 high × 5 wide	152	116	88th	54	36
Small fruit bodies	below 20	1·5–4 high × 1·5–3 wide	142	90	80th	54	52
Perstipitate fruit bodies	18–37	Stem 25–35 high Pileus 4–12 wide	144–168	108–120	96th–108th	46–54	36–4

Time in hours. Size in millimetres.

72 hours = 3 days, 96 = 4 days, 120 = 5 days, 144 = 6 days, 168 = 7 days, 192 = 8 days, 216 = 9 days.

I found no indication how the primordia are timed to expand during the night. No primordia ever expanded during the daytime though they began to develop at any hour. The time when expansion starts varies slightly because the pilei of similar fruit bodies may be a third, a half or two-thirds open on the following morning. With primordia developed naturally, one might expect a process requiring so much water to take place at night when the air is saturated and dew is forming, but I grew fruit bodies under a bell-jar in an atmosphere continuously saturated and others under a dripping tap with a film of water flowing over the wood, and expansion occurred only at night. The humidity of the air cannot therefore be a primary factor and one must suppose that the process is conditioned by temperature or light, and that the primordia on reaching a certain stage in development become sensitive to this stimulus which arises at nightfall. It may be remarked here that Morquer found in *A. mucida* that abundant moisture was required for complete fructification and that fruit bodies grown in the dark were abnormal and sterile(17): yet Fischer raised fruit bodies of the same species in darkness which were normal except for the lack of pigment.

(My observations were made at sea-level in the tropics; the temperature averaged 80° F., ±8°, with sunrise and sunset about 6 a.m. and 6 p.m.)

The microscopic development of the fruit body

I have not worked out the hyphal system of the fruit bodies in detail, for the jelly on the primordium renders them difficult objects to handle and section, and one must use fresh material. But the origin of the different tissues and palisades is quite clear.

The primordial shaft. Before the pileus develops the subcylindric or subconical primordium is composed of hyphae directed more or less longitudinally, though they are closely entwined, and the apical growth of the hyphae at the distal extremity causes the apical growth of the primordium. The direction of apical growth is probably determined by a positive phototropism and thus the longitudinal arrangement of the hyphae, while the extent of apical growth, as already mentioned, may be determined by the intensity of light falling on the apex. The hyphae at the apex grow and branch monopodially: they are narrow, 2–3 μ wide, and the cells which they cut off are 8–16 μ long. The growth of the hyphae round the periphery of the apex slackens off and their terminal cells enlarge to 5–8 μ wide, becoming subclavate or subventricose as the distal or proximal part is most distended: their ends point obliquely outwards and from the subterminal cells short laterals, of few cells, may arise and the terminal cells of these are similarly arrested and inflated about the same level. The primordial shaft is thus thinly corticated with a loose palisade,

which becomes the palisade of the disc, or of the infra-annular portion of the stem in the perstipitate variety. The older cells composing the body of the internal tissue begin slowly to enlarge acropetally from the attachment plug, from a very early stage. The structure of such a primordium before apical growth is arrested is shown in Fig. 7 *a*; the cells in the lower part would already be 25–40 × 5–7 μ.

The pileus is initiated not by the arrest of apical growth of the primordial shaft but by an increased branching of the hyphae in the interior shortly below its apex. The laterals arise mostly from the central longitudinal hyphae about 100 μ below their apices, and they grow out in all directions between the other longitudinal hyphae, surrounding them or pushing them aside; they branch profusely themselves and from a very compact subglobose mass of plectenchyma visible to the naked eye as a slight swelling. Within a few hours, the laterals on the proximal side of the swelling come into alignment as the growing margin of the pileus and proceed to build the limb; such a stage is shown in Fig. 7 *b*. Now, theoretically, the pileus is never exposed. Over its centre are the parts of the longitudinal hyphae distal to the regions where they gave off the laterals which build the limb, and these parts continue to grow apically for a considerable time longer: and on the outside of the incipient limb are the longitudinal hyphae which were pushed aside by the laterals, and also several hyphae which for some reason are stimulated to grow up from the cortex of the primordial shaft immediately below the incipient limb, and together these hyphae form a loose sheath round the margin. It is as if the head of the primordium were covered with hair from the first and its sides were surrounded by a high cravat, but, as this cravat is only one or two hyphae thick and as the hyphae are often loosely arranged, for such purposes as respiration and evaporation the margin of the pileus is practically exposed.

The hyphae at the margin of the pileus branch monopodially. They grow obliquely, outward from the apex of the stem and downward towards the base, so that the limb becomes deconic, but eventually they are directed more or less perpendicularly toward the surface of the stem and the extreme margin of the pileus is therefore slightly incurved, as in Fig. 7 *c*, and in Fig. 1. It is difficult to decide whether the curvature is brought about by a directional growth of the hyphae or is merely a mechanical effect of the very considerable multiplication of hyphae going on over the surface of the pileus at the same time, which tends to force the limb downward on to the stem in much the same way that the development of the cortex in the apothecium of Discomycetes forces the margin upward and inward.

While the margin of the pileus grows as a very compact ridge within the tenuous sheath surrounding it, many hyphae grow out from the upper surface of the limb just behind the margin and interweave with

Fig. 7. Diagrams of the early structure of the primordium: *a*, the primordial shaft; *b*, with the limb just forming; *c*, with the palisades, the gelatinous layer, the limb and the gill cavity established.

those of the sheath which, as already mentioned, have grown up from the loose palisade of the primordial shaft. In reciprocal manner more hyphae grow out from the surface of the stem near to the margin and interweave with those excrescent from the pileus. Thus an anastomosis between the loose palisade on the pileus and that on the stem takes place at the margin of the pileus at an early stage, some twelve hours after the inception of the limb, and the conjoint tissue forms the marginal veil. It is thin and rather scanty yet strong enough to hold the margin of the pileus until the night of expansion. Consequently, as the pileus increases in size by marginal and intercalary growth, the limb arches upward and outward and the narrow space between it and the stem is enlarged into the gill cavity.

Meanwhile, the ends of the original longitudinal hyphae at the apex of the primordium continue to grow out beyond the pileus. They branch frequently and they are joined by other narrow hyphae excrescent from the limb. At an early stage, so soon even as the pileus is started or shortly after, the walls of these hyphae become mucilaginous and the pale umber pigment appears in their cell sap, and so long as the margin of the pileus grows it gives off similar excrescent hyphae, some of which, as just described, contribute to the marginal veil. When the pileus is 0·5–1 mm. high, the outgrowth of these hyphae is arrested; their apices turn aside and interweave a little before the terminal cell enlarges and becomes subclavate or subventricose. Much sympodial branching then occurs from their subterminal cells: the laterals consist of a few cells only and in turn their apical growth is arrested and their terminal cells enlarge. Thus the primordial pileus becomes covered with a convex pad of gelatinous tissue bounded at the free surface by a palisade of subclavate or subventricose cells: these cells gradually elongate and the layer forms the external palisade of the pileus; it is incipient in Fig. 7 *c*.

During the period of intercalary growth of the pileus, which lasts until the final stage of expansion, narrow hyphae, 2–3 μ wide, continue to grow out into the jelly from the surface of the limb. Some reach the external palisade where they form pileocystidia, but most, and in later stages probably all of them, do not reach a greater length than 100 μ before their apical growth is arrested, when they branch sympodially from the proximal cells and the laterals grow up more or less parallel with the parent hyphae to the same level or are stopped at shorter distances. Thus is constructed the internal palisade of the pileus.

The jelly imbibes the drops of rain and dew which settle on the pileus. It swells and stretches the external palisade, despite the inflation of its cells, and the primary hyphae traversing the jelly are pulled out and become tenuous and not more than 1–2 μ wide in the mature tissue. The dome of jelly acts as a resilient buffer and as a screen against evaporation; one might almost call it amniotic.

The gills. The gills arise on the proximal side of the limb as ridges radiating from the apex of the stem. The primary gills are started shortly after the limb itself and in such a stage as Fig. 7 *c* they would already be visible as slight flutings: according as they start some distance down the stem or from the extreme apex so they are adnate, adnexed or nearly free in the mature fruit body. As they proceed radially following the limb, they diverge and at a certain distance apart the secondary gills are started in the widening intervals: after the gills have again diverged to the same extent the tertiaries are started and finally, in large pilei, quaternaries may be intercalated. The gills do not reach the extreme margin of the limb; there is a smooth narrow zone at the periphery, corresponding to the pore field in polypores, to the proximal border of which the gills can be traced. The slit between the limb and the stem, into which the gills project, is at first more or less open to the exterior, being loosely fenced round by the hyphae of the sheath: on the development of the veil it is closed into an annular cavity. The cavity enlarges through the arching of the limb but the gills grow so rapidly that it never appears as more than a slit in radial section, and eventually the edges of the gills are pressed against the stem on to which they imprint faint longitudinal striations.

In such a stage as Fig. 7 *c*, the under side of the limb, bordering the gill cavity, consists of a very compact palisade of down-growing hyphal ends, 3–5 μ wide, which extends from the stem apex to the margin. Apical growth is most rapid at the margin where the tissue of the limb is being formed. In the smooth narrow zone corresponding to the pore field, apical growth slackens and eventually stops, whereon the hymenium is constructed by sympodial branching. But along the lines of the gills outgrowth is stimulated afresh: linear radial growing regions are formed similar to that at the margin, and they are the edges of the gills. Along the edges of the young gills there is certainly an apical growth of the hyphae by which they are built out into the gill cavity, the proximal parts of the hyphae forming the trama of the gill. But I was unable to determine the exact manner of growth. The hyphae may be persistently monopodial or, as it sometimes seemed, they may form a kind of sympodium in which apical growth slows down after a few cells have been cut off and then a lateral grows up vigorously and pushes the original apex aside. Just as at the margin of the limb, however, apical growth slows down on either side of the growing region. The hyphal ends on the flanks of the gills are pushed aside by the upgrowing laterals and they come to point at right angles to their original direction, perpendicularly to the longitudinal hyphae in the trama. They then construct the hymenium. They cut off two or three short cells, after which the terminal cell becomes a basidium. The subterminal cells put out laterals which

grow directly or by devious routes between the primary hyphal ends and finally range themselves alongside after cutting off a few short cells; the terminal cell of the lateral then enlarges into a basidium and the subterminal cells branch in their turn. The terminal cells thus form the palisade of basidia and the subterminal cells form the subhymenium. The pleurocystidia also represent modified hyphal ends displaced from the gill edge, but in their case the terminal cells fail to cut off subhymenial cells but elongate directly into pleurocystidia: in sections of mature gills, therefore, the pleurocystidia are seen to arise from the trama and to pass through the subhymenium by means of a long stalk.

The cheilocystidia do not develop until the apical growth of the hyphae along the gill edge has been completed. The terminal cells of the hyphae then enlarge and become clavate, and, by branching from the subterminal cells, other cheilocystidia are intercalated in the same manner as the basidia on the sides of the gills. A wide compact sterile edge is thus formed.

Until the night of expansion, the basidia remain immature with clear, partly vacuolate contents. During that night they become densely and coarsely granular from minute oil drops formed throughout the cytoplasm. By 6 a.m. next morning some have already matured, and in an hour sporing is copious. The primary basidia mature in an acropetal sequence which spreads rapidly in a slanting wave from the centre of the pileus to the margin and from the bases of the gills to their edges. The secondary basidia then develop and mature over the whole hymenium without grouping: in any part, widely spaced mature basidia may be seen with young basidia in all stages of development around them. As the basidia are monomorphic and the gills are aequihymeniiferous, the fruit bodies belong to Buller's *Armillaria* subtype(6).

The spores arise as small subglobose or broadly pip-shaped swellings placed rather obliquely at the ends of the sterigmata and they have a blunt apiculus which projects from their base on the adaxial side. The contents are clear or slightly cloudy at first, but when the spores are about half-grown some of the oily granular cytoplasm from the basidium flows into them and fills up the interior except for a clear thin hyaline parietal layer. When the spore is full grown the wall thickens.

The pleurocystidia develop as gradually as the basidia. They are subcylindric at first, and as they grow beyond the level of the hymenium they become pronouncedly clavate with a long stalk and are shaped exactly like the cheilocystidia. They keep this shape while slowly growing larger until the morning before the night of expansion, when they elongate further by protruding the apical part and so become ventricose. They are largest and best formed at the base of the

gills in the central part of the pileus, where they have had longest to develop. Near the edges of the gills many of them persist in stages intermediate between the clavate and the ventricose. These transitions suggest that the cheilocystidia also, which have the shape of the young pleurocystidia, would become ventricose if given long enough to develop freely: as they are the last hymenial elements to be formed, shortly before the maturing of the basidia and the expansion of the fruit body, their growth is naturally arrested.

Both kinds of cystidia have clear vacuolate contents. Of all the cells in the fruit body only the basidia and spores have the oily granular contents. The oil droplets must be the reserve form of fats transferred in soluble components from the mycelium, precipitated in the basidia and then passed into the spores, in which state they remain until resolution on germination.

The stem. The inception of the pileus terminates the apical growth of the stem, the subsequent increase in length of which is due to vacuolation and elongation of the cells: the length of the primordial stem cannot therefore exceed 1–2 mm. in the typical form. It thickens also by branching of the hyphae and laterals arise especially from the surface which forms the inner wall of the gill cavity. They project shortly into the cavity, but the terminal cells soon enlarge, becoming clavate or ventricose, and then, by rather infrequent sympodial branching, a loose irregular cortex is constructed similar to that on the disc. The cortex can develop only where the gills are not pressed against the stem, and so it is thickest just above the veil and reduced towards the apex. Where the margin of the pileus touches the stem, the excrescent laterals interweave with the excrescent hyphae from the pileus to strengthen the veil, but there is no anastomosis between the edges of the gills and the palisade on the stem.

During the growth of the primordium the hyphae begin to enlarge slowly. The vacuolation of the cells, as already mentioned, proceeds acropetally from the plug to the extremity of the pileus and the gills. The rate of enlargement of the cells gradually increases, reaching a maximum on the night of expansion, and then gradually declines. The extent of enlargement of the cells also increases gradually in acropetal sequence to the centre of the pileus, except for the special region of curvature at the stem apex, and declines towards the extremities. The grand period of most rapid enlargement coincides in the typical form with the expansion of the region of greatest enlargement, which includes the supra-annular portion of the stem, the centre of the pileus and the proximal parts of the gills, and thus the nocturnal opening of the fruit body. The period of both dies away gradually and the limb and the gills are strongly attenuate centrifugally. In the perstipitate variety the grand period of both processes

is more extensive and the primordium is less perfect. Even after the enlargement of the hyphae the pileus may still flatten further through the intercalary growth of the hymenium, but as the basidia develop rapidly and collapse on shedding the spores this process is not as effective as in many other toadstools, and the pileus, though often plane, is never revolute.

The enlargement of the terminal cells in the superficial palisades proceeds independently of that of the medullary hyphae of the same part. The first terminal cells to enlarge are those in the palisade on the disc. Then follow those in the external palisade of the pileus and, shortly after, the first basidia and pleurocystidia, and lastly those in the palisade on the supra-annular portion of the stem. The terminal cells in the palisades begin to enlarge many hours before the corresponding medullary hyphae. The process depends on local conditions and is not part of the general motor mechanism of the fruit body.

The size of the fruit body

Are the undersized fruit bodies, which occur in *Collybia apalosarca* and many other agarics, juvenile forms of the normal ones or are they merely less inflated? Do they consist of fewer cells, that is, or have their cells not enlarged so much? One cannot decide from macroscopic evidence because the size of the mature fruit body is determined by three distinct processes, each of which is microscopic. In the first place, the length of any part is determined by the extent of apical growth of the constituent hyphae, *i.e.* the length depends on the number of *cells* composing the constituent hyphae: this is the property which enables one to determine directly whether a fruit body is juvenile or not, since a juvenile form is one whose growth is arrested before reaching the normal limits of the species and which matures in this state. Secondly, both the length and the width of any part depend on the amount of enlargement which the cells undergo: this is the most striking property but the one with the least morphological or evolutionary significance. Thirdly, the width and, to a small extent, the length depend on the amount of intercalary growth by branching, *i.e.* on the number of *hyphae* composing the part.

The first property is very difficult, if not impossible, to measure. In an ideal primordium with indirect development, which has firstly a period solely of apical growth and then a period solely of enlargement, it should be sufficient to measure the length of any part before enlargement begins, divide by the average length of the cells, and so arrive at the number of cells in a primary longitudinal hypha and thus the extent of apical growth. But, except perhaps in the Phalloidaceae, no primordium is so perfect. It is impossible with the primordia of agarics to decide exactly when apical growth has ceased and at what

stage therefore the measurements should be taken, and there is always some enlargement proceeding acropetally from the base from the inception of the primordium: apical growth and cell enlargement coincide in some degree from the first though maximum enlargement is delayed until apical growth has ceased. (When the primordium is poorly differentiated and develops directly, as in *Cantharellus* or *Clavaria*, the two processes are concurrent for a long time until the fruit body is half-grown or more.)

But the second property can easily be investigated and it enables one to decide indirectly if the differences in size of the fruit bodies are due to early arrest of growth (juvenescence) or merely to different degrees of inflation. The average length of the cells of the motor tissue must be determined before and after enlargement. Then, for example, if two fruit bodies of different sizes have the same average enlargement, the smaller must be composed of fewer cells (deflate them and the smaller will be smaller because its hyphae have not

Table II

Fruit body	Length of stem mm.	Width of stem mm.	Average length of cells	Width of cells	Ratio of stem-lengths	Ratio of average cell-lengths
a	45	5·0	392	8–26	1	1
b	40	4·0	398	7–28	0·9	1·02
c	30	3·5	372	8–28	0·7	0·95
d	24	3·0	415	7–24	0·5	1·06
e	19	2·5	352	7–26	0·4	0·9
f	12	1·5	219	7–23	0·3	0·56
g	5·5	1·0	281	6–22	0·1	0·72

grown so much). On the other hand, if a fruit body is only half the normal size and has about half the normal average enlargement, the difference in size is merely one of inflation. Without analysis of this sort, little meaning can be attached to differences in size. No doubt, by integration, one could find an expression for the degree of enlargement of the whole fruit body, or of one part, and by dividing the mature length by the average enlargement so determine the length due to apical growth: in any part, as the stem, the gills or the limb, all the cells do not enlarge to the same extent, the proximal ones tending to enlarge more than the distal.

In Table II the results of measuring the cells in the stem of seven fruit bodies are given: three of the fruit bodies were fairly large, two of medium size, one small and one very small. Only the cells in the region of greatest enlargement were measured, that is in the medulla of the middle third of the stem in a shell extending from 50 μ inside the surface to 1000 μ: the average enlargement is taken from thirty measurements. The length of the stem was measured from the top of the disc to the apex and the width was measured immediately above

the disc, for the disc which scarcely elongates must be reckoned separately; the sections were mounted in water. I have assumed that the average initial length of the cells was always the same; one cannot, of course, measure them before and after expansion in the same fruit body, nor can one tell from the appearance of the primordium at the early stage when the initial lengths must be measured what its final size will be: but in many primordia I found them to be about 12 μ long when first cut off from the apical cell, and this average holds widely in many Basidiomycetes.

Take, for reference, the length of the stem in the largest fruit body, *a*, as unity and let x be the average number of cells in each primary longitudinal hypha in its stem. Then, as the cells in the stem of the fruit bodies *a*, *b*, *c*, *d*, *e*, all enlarge to much the same extent each primary stem hypha in *b*, *c*, *d*, *e*, consists of $0{\cdot}9x$, $0{\cdot}7x$, $0{\cdot}5x$, $0{\cdot}4x$ cells respectively, and these fruit bodies can be regarded as a series of juvenile forms in which apical growth of the axis has been arrested successively at earlier stages. Fruit body *g* is also an exceedingly juvenile form, but its cells have enlarged only to three-quarters of the average value. Fruit body *f* presents the alternative possibility: it is small chiefly because its cells have enlarged only to half the average extent though it is probably juvenile also in some degree. The argument that small fruit bodies are juvenescent will be supported by other data in the next section.

The explanation thus obtained for the length of the stem will probably apply also to the pileus because there is a close relation between the length of the mature stem and the width of the mature pileus; a fruit body with a long, massive stem has generally a wide pileus and one with a short stem has a small pileus. In the development of the gills, however, the third property becomes important. The cells of the tramal hyphae enlarge, too, during the expansion of the primordium, but in the mature fruit body they are pulled apart and stretched by the intercalary growth of the hymenium. This property thus prevents the simple comparison between the lengths of the tramal cells and the width of the gill in fruit bodies of different sizes, for allowance must be made for differences in intercalary growth which would be exceedingly difficult to estimate. Nevertheless, the explanation given for the size of the stem and the pileus will probably apply in some degree to the gills also, so that when a fruit body has a small pileus and a short stem through juvenescence, the gills will probably be narrow for the same reason.

A variety "minor" for small fruit bodies, without other qualification, is therefore untenable in this species, because the size of the fruit body is determined by two distinct processes apart from any effects of malnutrition or excessive evaporation.

The arrangement of the gills

The number of primary gills in a fruit body depends on the width of the stem apex and the number of gill ranks upon the width of the pileus. In Tables III and IV are compiled the results of counting and measuring these properties in twenty-five fruit bodies.

Fruit bodies with small pilei and narrow stems have the fewest ranks and the fewest primaries. Among the arbitrary size groups which have been made, the small fruit bodies have 1–2 or 2–3 ranks with 11–20 primaries; the medium-sized fruit bodies have 3 or 3–4 ranks with 18–25 primaries; the large fruit bodies have 3–4 or 4 ranks

Table III

Ranks of gills										
1–2 or 2	Width of pileus in mm.	4	5	6	8	14	17	21		
	No. of primaries	12	11	17	11	15	20	15		
2–3 or 3	Width of pileus in mm.	10·5	18	18	19	20	20	22	28	
	No. of primaries	14	19	20	19	18	13	19	18	
3–4 or 4	Width of pileus in mm.	36	42	45	65	72	74	76	86	89	93
	No. of primaries	31	23	25	30	30	31	28	32	26	29

Table IV

Width of stem apex in mm.							
0·5–1	No. of primaries	11	11	12			
	Width of pileus in mm.	5	8	4			
1·1–1·9	No. of primaries	13	14	15	15	17	18
	Width of pileus in mm.	20	10·5	14	21	6	20
2–3	No. of primaries	18	19	19	20	20	
	Width of pileus in mm.	28	19	22	17	18	
4–6	No. of primaries	23	25	31	31		
	Width of pileus in mm.	42	45	36	74		
7–8	No. of primaries	26	28	29	30	30	32
	Width of pileus in mm.	89	76	93	65	72	86

with 26–32 primaries. Now this shows that fruit bodies with small pilei, and small fruit bodies generally, therefore, are juvenescent. The number of ranks is a measure of the marginal growth of the pileus. The intercalation of a new rank follows on divergence of the preformed gills as they grow centrifugally with the margin of the pileus. If, therefore, marginal growth is stopped prematurely, the pileus even on expansion will have but few ranks: or, other things being equal, the greater the extent of marginal growth of the pileus the greater the number of gill ranks.

There is doubtless in each species of agaric a *spacing factor* which determines the proximity and succession of the gill ridges. The factor must be a function chiefly of the thickness of the ridges, but to determine its value observations would have to be made on unexpanded primordia. The gills are started in a region without expansion and

their original arrangement may be greatly distorted in the mature fruit body owing to the unequal enlargement of the parts. It would be necessary also to determine the inclination of the limb to the stem in the primordium and the effect of incurvature of the margin in estimating the centrifugal growth of the pileus, and to determine the amount of intercalary growth in the stem, for on this depends the size of the primordial stem apex and thus the number of primaries which it can accommodate. For such a tedious investigation the material would have to be much simpler and easier to handle than the primordia of *Collybia apalosarca* and the species of *Lentinus* with coriaceous flesh suggest themselves because they are gymnocarpic with direct development.

Collybia radicata

The Malayan material of this species differs macroscopically from the European and North American in the following respects:

The pileus is subhygrophanous with the surface dry and not viscid; old pilei become slightly viscid in decay.

The stem is clothed, except for the apex, with fuscous or light brown adpressed fibrils or scurfy particles, and sometimes it is adpressedly fibrillosely squamulose.

The habit is solitary, rarely two to three fruit bodies together, and always terrestrial from buried roots.

These are the numerical and microscopic data so far collected for the Malayan material:

Pileus 1–12 cm. wide. Stem, above ground, 6–14 cm. × 3–8 mm. at the apex, × 5–16 mm. at ground-level; below ground up to 16 cm. long, tapering to a white mycelial strand, 0·5 mm., connected to the substratum. Gills in 3–5 ranks, mostly 3–4, with 13–28 primaries 4–10 mm. wide.

Spores 11·5–15·5 × 11–14 μ (Pahang specimens), 15–19 × 12–15 μ (Brastagi specimens); wall *ca.* 0·3 μ thick.

Basidia 58–75 × 13–18 μ, with 4 sterigmata 6–10 × 3–4 μ at the base, or in some fruit bodies with only two sterigmata 9–13 × 4–6 μ (rarely with a small third sterigma, sterile or with an abortive spore).

Pleurocystidia 80–150 × 18–38 μ, as in *C. apalosarca*, but mostly clavate-stipitate in some fruit bodies and mostly ventricose-stipitate and prolonged in others.

Cheilocystidia as in *C. apalosarca*, but many subventricose with slightly tapered apex.

The microscopic structure is similar to that of *C. apalosarca*, there being a similar formation of palisades and cystidia, but the structure of the pileus is simpler, there being no jelly or veil, and the palisade on the stem is better developed.

The pileus. There is a single palisade on the pileus. It has a different composition in the centre from over the limb where, as shown in Fig. 8, three elements can be distinguished. Firstly, there are long colourless thin-walled pileocystidia, 70–180 μ long; their proximal portion, 30–60 μ long, is usually subventricose, 4–12 μ wide, and the free terminal portion is filiform, straight or flexuous, 2–3·5 μ

Fig. 8. A part of the palisade from the centre of the pileus of *Collybia radicata*: × 500.

wide, and occasionally 1-septate. Secondly, there are large clavate, or subventricose, thin-walled pileocystidia, 40–70 × 8–20 μ, which form the body of the palisade on a level with the subventricose portions of the first elements: they appear like sterile basidia but they are simply vacuolate, not oily granular, and occasionally they contain the pale umber pigment. Thirdly, small clavate, or subcylindric, thin-walled pileocystidia, 15–40 × 5–12 μ, with the pale umber pigment in

their cell sap: these elements are packed between the stalks of the other two, so that the whole palisade appears to rest on a deeply pigmented layer. It seems that these three elements have developed successively by sympodial branching of the terminal hyphae. The long colourless pileocystidia are probably the first-formed elements derived from the ends of the primary hyphae of the primordial shaft on inception of the pileus. Of their laterals, some may develop similar pileocystidia but probably most develop the large clavate colourless elements. Then, in turn, these give rise to the small clavate pigmented elements, which are thus the shortest because they are the youngest.

Fig. 9. A part of the palisade from the distal half of the limb of *Collybia radicata*: × 500.

Over the limb the palisade consists almost exclusively of large clavate pileocystidia, 25–75 × 10–30 μ, with clear umber sap (Fig. 9). Their subterminal cells are more or less inflated and pigmented and the whole forms a pseudoparenchymatous layer thinning off to the margin of the pileus, where only the terminal cells are inflated. Colourless filiform pileocystidia, like the first elements of the palisade in the centre of the pileus, occur sparsely but they are absent from the peripheral part of the limb.

The pale umber pigment causes the colour of the pileus as in *C. apalosarca*. The large size and rounded ends of the pileocystidia over the limb cause its innately pruinose appearance. The slight viscidity

of the old pilei is due to the collapse and mucification of the long colourless pileocystidia.

The stem. On the surface of the stem are clumps of excrescent hyphae projecting up to 200 μ, as in Fig. 10. The terminal cells are inflated, clavate or subventricose, 25–75 × 8–25 μ, and the subterminal cells are also more or less inflated and sparingly branched. The cells are widely vacuolate and often contain the umber pigment. On the primordial stem there is evidently a continuous loose palisade,

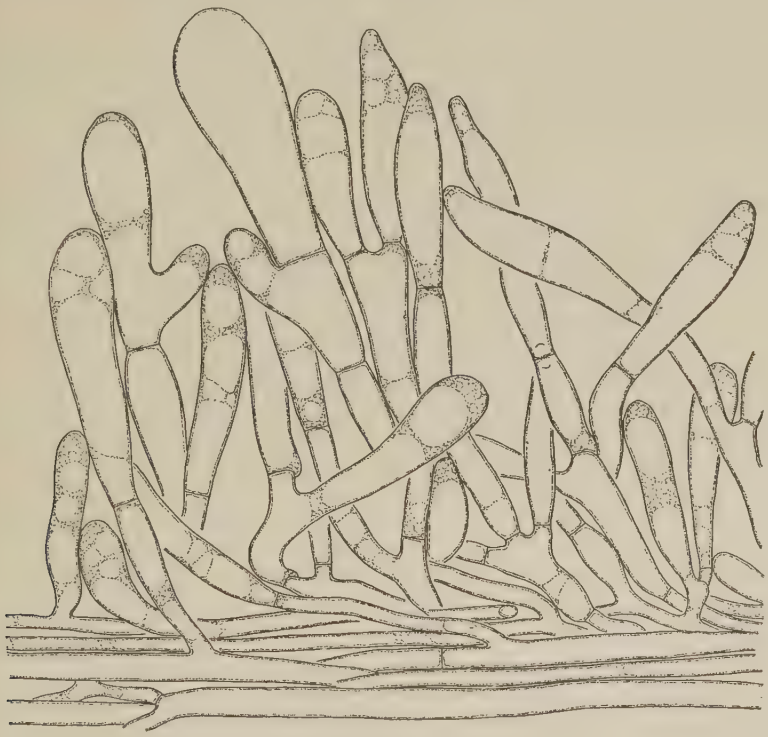

Fig. 10. A part of the palisade from the stem of *Collybia radicata*, about 1 cm. below the apex: × 500.

which is reduced toward the apex, and on expansion it is broken up into the clumps of hyphae.

The umber pigment in the excrescent hyphae and in many of the superficial medullary hyphae causes the colour of the stem: the fibrillose and squamulose markings are caused by the disruption of the palisade.

Collybia altissima Massee (*Kew Bull.* 1914, p. 358), based on a collection from the Botanic Gardens, Singapore, is synonymous with *C.*

radicata. I have not examined the type material, if there is any, but there is a painting of the original in the Singapore Herbarium which leaves no shadow of doubt: the spore characters given by Massee are probably quite erroneous.

The data on *Armillaria mucida*

I have extracted from Fischer's papers the mycological facts germane to this study:

The spores germinate within twenty-four hours in ordinary culture media. The mycelium is white but eventually becomes orange at the base of the Petri dish; on cubes of beechwood it also becomes light orange then blood red in patches. There are no conidia in artificial culture. The air-dried spores do not retain their viability for more than six weeks.

When the spores were germinated on beer-wort jelly and then transferred to sterilised bread, the first fruit bodies began to develop after sixty days and matured in eight days; from spore to spore the life cycle took sixty-eight days.

When the spores were sown directly on sterilised bread, the first fruit bodies appeared after forty-five days and matured six days later, thus giving fifty-one days from spore to spore.

When the mycelium was transferred from bread cultures to cubes of beechwood, the first fruit bodies matured 109 days after the spores had been germinated.

No fruit bodies were produced in cultures on beer-wort jelly.

In culture, the primordia developed in large clusters as small conical protuberances. In twenty-four hours the pileus was started. On the fourth or fifth day the primordia were well grown and began to stretch the veil. On the sixth to the eighth day the veil ruptured and the pileus expanded. The elongation of the stem is conspicuous from a very early stage (as in *Collybia apalosarca* var. *perstipitata*). There are no records on the exact time of rupture of the veil or on the period of maturity. The fruit bodies raised in culture were smaller than the wild ones, their pilei not exceeding 5 cm. wide and their stems being slender and more elongated.

The fruit bodies were grown mostly in the dark. If kept in continuous darkness the pilei were white; if grown in light, the pilei were dark brown at first becoming paler at maturity. If young primordia were transferred from darkness to light, they coloured up, but those transferred in later stages remained white. The fruit bodies matured equally well in darkness as in light.

In one culture there developed an irregular tremelloid fructification without a stem but with a normal fertile hymenium on the folds.

Development is angiocarpic. The primordial shaft has evidently the

same structure as that of *C. apalosarca*. But when the pileus is started, it is said that a layer of hyphae, parallel to the surface and two to three hyphae thick, covers the whole primordium: it is the universal veil, which becomes gelatinous at a later stage to form the slimy covering of the pileus and the infra-annular portion of the stem. When the pileus has formed, there is a layer of radiating hyphae distal to it which appears equivalent to the gelatinous hyphae in *C. apalosarca*. The gill cavity arises schizogenously between the limb and the stem and the marginal veil is formed from the "neutral" ground tissue left over in this part. When the pileus expands the universal veil has disorganised into the slimy covering and the marginal veil is pulled from the pileus to form the ring on the stem, which the author, wrongly surely, calls a superior annulus. The spores may ripen before the veil ruptures.

Fischer's interpretation of the development is scarcely borne out by his figures which show that his material was badly crumpled and distorted owing to fixation: the sections are oblique and the palisades therefore appear stratified with many layers of cells.

A close comparison between the rate of development of the fruit body in *Armillaria mucida* and that of *Collybia apalosarca* is scarcely possible as yet, since Fischer's material was raised in artificial culture, mostly in the dark, and the average temperature of the surroundings, which is not mentioned, could hardly have exceeded 20° C. unless an incubator was used. But a comparison with the fruit bodies of *C. apalosarca* var. *perstipitata*, which were raised on wood under natural conditions at an average temperature of 27° C., and which took four and a half to five days to reach maturity, suggests a doubling of the rate of development for a rise of 10° C., so that at the same temperature both should have the same rate.

Furthermore, Boursier(3) describes the presence of large cystidia, up to $200 \times 40\,\mu$, on the sides and edges of the gills, the presence on the pileus of a compact palisade of clavate cells with more or less mucilaginous walls, and large oil drops in the basidia and the spores but not in the cystidia, which are simply vacuolate. Rea(22) also describes the cystidia on the gills as abundant, hyaline, fusiform or cylindric, 90–140 (–180) × 15–30 (–45) μ.

The comparison between *Collybia radicata*, *C. apalosarca* and *Armillaria mucida*

The size of the fruit body in all three varies roughly between the same limits: *Armillaria mucida* has on the average the smallest because the pileus does not exceed 10 cm. in width (according to published descriptions), and it may attain 15 cm. in the other two. So far

as possible at present, the points of agreement may be stated as follows:

(1) The pileus is dark fuscous brown or umber at first, becoming pale brown or greyish brown on expansion and finally pallid white, the colour being due to a pale umber pigment in the cell sap. In all three, very pale or colourless specimens may occur. It seems from the work of Fischer and Morquer that light is required for the development of the pigment.

(2) The mature pileus is plane or gibbous, not revolute or infundibuliform.

(3) The margin of the pileus is slightly incurved at first.

(4) The stem is stout, fibrous and homogeneous with the pileus.

(5) The gills are subdistant, broad, rather thick, waxy or submucilaginous, white, with a slight decurrent tooth and with a broad sterile edge: they become powdered with the spores.

(6) The flesh is white, rather soft, subhygrophanous, rather rapidly putrescent, fairly thick in the centre of the pileus but membranous in the distal part of the limb.

(7) The spores are white, large, subglobose or broadly ellipsoid, about 16μ wide, multiguttulate, and with a fairly thick wall, *ca.* $0{\cdot}5\mu$. The basidia are correspondingly large, *ca.* $65 \times 20\mu$, and multiguttulate.

(8) The cystidia are large, smooth, thin-walled, vacuolate and abundant: the pleurocystidia are mostly ventricose, *ca.* $150 \times 30\mu$, the cheilocystidia mostly clavate and smaller, *ca.* $80 \times 20\mu$, though the cheilocystidia have not definitely been described in *A. mucida*.

(9) There is at least one compact palisade on the pileus, and there is probably a loose palisade of caulocystidia.

(10) The mechanism of the fruit body is Buller's *Armillaria* subtype.

(11) The mycelium is saprophytic on wood.

They differ in these respects:

(1) **The pileus.** A single palisade occurs in *Collybia radicata*, two in *C. apalosarca*. The gelatinous layer of *C. apalosarca* is absent from *C. radicata*. *Armillaria mucida* has probably both palisades with included jelly.

(2) **The stem.** The palisade in *Collybia radicata* differs from that on the supra-annular portion of the stem in *Collybia apalosarca* in the marked inflation of the subterminal cells and the presence of the umber pigment in many of them. Information about *Armillaria mucida* is lacking.

The surface of the infra-annular portion is viscid in *A. mucida* though the cause is uncertain: it is dry in the other two.

The motor tissue lies in both infra-annular and supra-annular portions in *A. mucida*; this state, which is usual in agarics, can be called the "*perstipitate*." In *Collybia apalosarca typica* the motor tissue is

confined in the supra-annular portion, and this state may be called *supra-stipitate*, cf. *Amanita* and *Volvaria*. *Collybia apalosarca* var. *perstipitata* agrees with *Armillaria mucida*. *Collybia radicata* is perhaps intermediate between the two extremes although it is impossible to say definitely before the primordia have been examined. This relation is shown in Fig. 11.

There is a disc in *C. apalosarca typica*, absent from the others, although there is a distinct swelling of the stem at a corresponding level in *C. radicata*, *i.e.* at ground-level where "root" and stem join.

(3) **The root.** It is best developed in *C. radicata*. It is reduced to a microscopic plug in *C. apalosarca typica* and var. *perstipitata*: this, too,

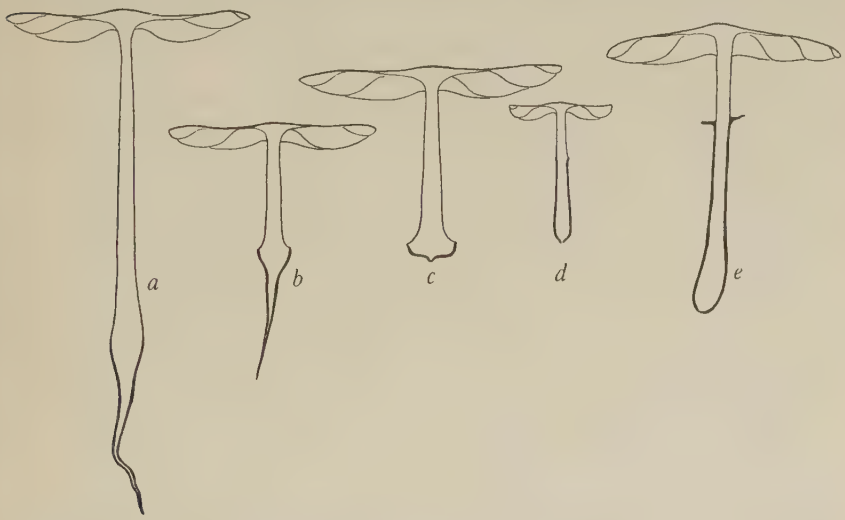

Fig. 11. Sagittal sections of mature fruit-bodies: *a*, of *Collybia radicata*; *b*, of *C. apalosarca* f. *radicans*; *c*, of *C. apalosarca typica*; *d*, of *C. apalosarca* var. *perstipitata*; *e*, of *Armillaria mucida*; the portions of the stem homologous with infra-annular portion in *A. mucida* shown by a heavy line.

must be the condition in *Armillaria mucida* and the rootless form of *Collybia radicata* described by Lange (16). In *C. apalosarca* f. *radicans* the root is often as well developed as in *C. radicata*. It is an opportunist growth made when the primordial shaft has a considerable distance to cover before the pileus can be developed, and it is not a primary distinguishing character. The emergency is nearly always present in some degree in the fruiting of *C. radicata*: in Lange's rootless form the fruit bodies developed on exposed roots and had a slight swelling at the base of the stem.

(4) **The gills.** In *C. radicata* they are widely sinuato-adnexed and often almost free. In *Armillaria mucida* they are rounded adnate or

subdecurrent. In *Collybia apalosarca* in Malaya they are as often rounded adnate as adnexed, sometimes widely sinuate and occasionally nearly free, but Petch makes a point that they are either adnate or sinuato-adnate in Ceylon.

(5) **The veil.** In *C. radicata* there is apparently no veil. In *C. apalosarca* it is rudimentary and leaves only a faint ridge or zone on the stem. In *Armillaria mucida* it is well developed and breaks away from the margin of the pileus to form an inferior annulus on the stem.

(6) **The spores.** *Collybia apalosarca* has the largest spores, those of *C. radicata* being the same size as those of *Armillaria mucida* or a trifle smaller. But in all three there is so much variation that I have tabulated the measurements given by different authors (Table V).

Table V. *Sizes of Spores in* μ.

Authority	*C. radicata*	*A. mucida*	*C. apalosarca*
Bresadola (*Ic. Myc.*)	12–18×9–12	—	—
Buller (*Fungi of Manitoba*)	9–12×6–7 (*C. radicata* var.)	—	—
Corner	11·5–19×11–15	—	16–23×16–22
Fischer	—	14–16×8–9	—
Killermann (*Nat. Pfl. Fam.*)	12–16×10–12	14, globose	—
Lange (*Ag. of Denm.*)	15×10	13–18×12–16	—
Lloyd (*Myc. Notes*, III)	15–17, globose	—	—
Massee (*Eur. Fung. Flor.*)	14–15×8–9	15–16×8–9	—
Murrill (*N. Am. Flor.*)	15–17·5×10–12·5	—	—
Petch	—	—	16–24, globose
Rea (*Brit. Bas.*)	14–15×8–9	15–17, globose	—
Ricken (*Die Blätt.*)	12–16×10–12	15–18, subglob.	—

In *Collybia apalosarca*, fruit bodies in one collection generally have the spores of the same size, 16–19 μ or 19–21 μ or 21–23 μ, so that the variations may be hereditary.

In *C. radicata* and *Armillaria mucida* they are often ellipsoid rather than globose.

(7) **The cystidia.** As already mentioned, the pleurocystidia in the Malayan material of *Collybia radicata* are clavate rather than ventricose and the cheilocystidia are subventricose rather than clavate. *C. radicata* var. *gracilis* Lange has the cystidia (? pleurocystidia), small and narrowly ventricose, *ca.* 40 μ long × 2–3 μ wide at the apex, but the

details are not clear. Exact description of the cystidia in *Armillaria mucida* is also lacking.

(8) **The manner of growth.** The fruit bodies in *Collybia radicata* and *C. apalosarca* generally develop singly and may be solitary or in troops. In *Armillaria mucida* they are tufted, *i.e.* many primordia arise close together and, developing equally, become connate at the base. Occasionally in *Collybia apalosarca* small tufts are formed, but usually when the primordia are so crowded one takes the lead and the others abort. The smaller average size of the fruit bodies in *Armillaria mucida* may result from the tufted habit.

(9) **The habitat.** The fruit bodies of *Collybia apalosarca* and *Armillaria mucida* develop on dead trunks and branches above ground. Those of *Collybia radicata* develop from dead roots, which are generally buried, and they appear therefore terrestrial, but they are not humicolous: sometimes they grow from the top of stumps, but on following the "root" it is found to pass through the upper rotten wood and arise from the xylem of the tree roots, and they have never been recorded as growing from standing or fallen trunks.

(10) **Geographical distribution.** *C. radicata* is evidently cosmopolitan, occurring throughout the north temperate zone, Africa, Ceylon, Malaya, Java and Australia. *C. apalosarca* has been found hitherto only in Ceylon, Java and Malaya and is clearly tropical. *Armillaria mucida*, on the other hand, appears to be a temperate species occurring in North America and Europe.

Now, admitting the following general propositions about the evolution of agarics, the interrelations of the three species can be interpreted phylogenetically:

(1) A single palisade on the pileus is a less advanced character than two palisades with included jelly.

(2) As indirect development is derived from direct development (8), so the restriction of the motor tissue of the stem to the supra-annular portion and the modification of the infra-annular portion into a supporting disc are advances on the general condition in which the motor tissue is co-extensive with the stem and there is no disc; the supra-stipitate is derived from the perstipitate. (The supra-stipitate appears to lead to the "destipitate" condition of Gastromycetes, by total failure of the motor mechanism, cf. the Secotiaceae and the inarticulate Hymenogastraceae.)

(3) Decurrent gills precede adnate and adnate precede adnexed: free gills are the latest, as the hymenium is worked off the stem which becomes solely an elevator. Adnato-decurrent gills are intermediate between decurrent and adnate gills; sinuate gills are intermediate between adnate and adnexed or free gills.

(4) The gymnocarpic state is primitive, the angiocarpic advanced.

(5) Large spores are derived from the average ellipsoid spore, $6–8 \times 4–5\,\mu$.

(6) The humicolous habit precedes the lignicolous.

Firstly, therefore, taking each point in order, *Collybia radicata* is the least advanced; the other two are probably at the same level. The two states are not so different as they appear. With respect to the centre of the pileus in *C. radicata*, the long colourless pileocystidia are probably homologous with the primary mucilage hyphae in *C. apalosarca*; the large colourless clavate pileocystidia are probably homologous with the secondary mucilage hyphae and the terminal pileocystidia in the external palisade in *C. apalosarca*, and the small pigmented pileocystidia will then be homologous with the elements of the internal palisade in *C. apalosarca*. The two states differ chiefly through the modification of the primary hyphae of the palisade into mucilage hyphae in *C. apalosarca*.

Secondly, *Armillaria mucida* and *Collybia apalosarca* var. *perstipitata* are the least advanced: *C. apalosarca* is the most advanced and *C. radicata* is perhaps intermediate. That is to say, *C. apalosarca* has the best developed primordium. In connection with the stem, it may be remarked also that, if the development of mucilage hyphae on the pileus is an advance, so must be the mucification of the surface of the infra-annular portion of the stem in *Armillaria mucida*; it is a speciality, therefore, of *A. mucida*.

Thirdly, *Armillaria mucida* is the least advanced, *Collybia radicata* the most advanced, and *C. apalosarca* intermediate; but the differences are not great.

Fourthly, *C. radicata* is the least advanced, *Armillaria mucida* the most advanced, and *Collybia apalosarca* is intermediate.

Fifthly, *C. apalosarca* is the most advanced, having the largest spores, and *C. radicata* is the least advanced, especially in its variety from Manitoba, and *Armillaria mucida* is intermediate. The large multiguttulate spore in the three species must be derived from the small ellipsoid spores, $6–9 \times 4–7\,\mu$, with homogeneous oily contents, which is common in *Collybia* and the related genera *Tricholoma*, *Clitocybe* and *Hygrophorus*.

Sixthly, there is no obvious decision. The point is mentioned in order to notice that *Collybia radicata* is not humicolous but lignicolous and radicicolous, even though the fruit bodies are borne on the ground. It is most important to discover whether the immediate ancestor of this group was humicolous or lignicolous; if humicolous, cf. *C. platyphylla*, then *C. radicata* would present the first step toward the arboreal habitat of the other two; if lignicolous, then *C. radicata* must be specialised in being limited to roots.

On three out of five counts, therefore, in respect of the structure of

the pileus, the veil and the spores, *C. radicata* is the most primitive. On the other two counts, in respect of the differentiation of the primordium and the attachment of the gills, *Armillaria mucida* is the most primitive. In respect of the gills *Collybia radicata* is the most advanced; in respect of the veil, *Armillaria mucida* is the most advanced: and in both these respects *Collybia apalosarca* is intermediate. In respect of the primordium and the spores *C. apalosarca* is the most advanced.

Clearly, none of the three is on the direct line of descent; each is specialised. To relate them in the simplest way, it is necessary to postulate at least two ancestral species, which may be called the first and second hypotheticals. Their interrelations are shown in Fig. 12.

The first hypothetical would be gymnocarpic, perstipitate, caespitose, with adnate or decurrent gills, dry pileus and stem, a single palisade on the pileus, and broadly ellipsoid spores about $10 \times 7\,\mu$. The second hypothetical would differ in being hemiangiocarpic, *i.e.* with incipient marginal veil as in *C. apalosarca*, with two palisades

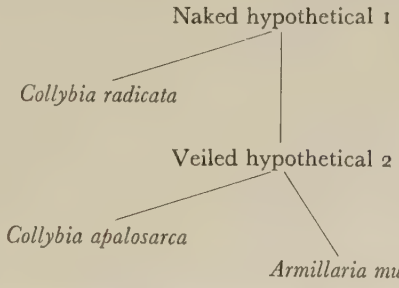

Fig. 12. The supposed genealogy of *Collybia radicata*, *C. apalosarca*, and *Armillaria mucida*.

with included jelly on the pileus and with the spores about $15 \times 12\,\mu$. *C. radicata* differs from the first hypothetical in the radicicolous habit, the sinuato-adnexed gills and the larger spores. *C. apalosarca typica* differs from the second hypothetical in being supra-stipitate with a disc formed from the infra-annular portion of the stem, in the larger spores and in the subgregarious or solitary habit: the development of the disc is connected with the change in habit, because solitary specimens of the perstipitate variety without the disc are unstable: the fruit bodies of the two hypotheticals would derive their support from mutual pressure in the tuft, as in *Armillaria mucida*. *A. mucida* differs from the second hypothetical in being truly angiocarpic with an inferior annulus, and in the viscid surface to the infra-annular portion of the stem: a third hypothetical with a ring but a dry stem might therefore be postulated.

Whether the first hypothetical were humicolous or lignicolous with the arboreal habitat, *Collybia radicata* in becoming radicicolous would pass out of competition. If with the arboreal habitat, then both *C.*

apalosarca and *Armillaria mucida* would compete with it as well as the second hypothetical, and as both are derivative and obviously successful, they will have ousted the hypotheticals from the eastern tropics on the one hand and the north temperate zone on the other hand. But the second hypothetical may survive in the American tropics or in the south temperate zone, and it may be found among Spegazzini's species. And if, though it seems unlikely, the first hypothetical were humicolous, it too may survive somewhere.

Related species

It is not difficult, in spite of no detailed information, to find other species which are closely related to these three, for example *Clitocybe atrialba* (Murr.) Kauff., *Collybia Henriettae* W. G. Sm., *C. longipes* (Bull.) Berk. and *C. cheimonophylla* Berk. & Curt.

C. atrialba occurs in the southern states of North America (14). It is very close to *C. radicata* and differs chiefly in the decurrent gills and small spores (so it may prove the first hypothetical). It is radicicolous. The fruit body has essentially the same build as that of *C. radicata*, with a dark brown pileus, brown scaly markings on the stem, broad white subdistant gills and white flesh: the spores are subglobose or broadly ellipsoid, 9–11 (–12) × 7–9 μ. The habitat suggests that other radicicolous species of *Collybia*, as *C. fusipes*, may be related either directly to the ancestral stock or from specialised offshoots, and perhaps even the humicolous (?) *C. platyphylla*, but these species may lack the palisades on the stem and the pileus. But if unrelated, whence have they come to this resemblance? *C. maculata*, which has a palisade of caulocystidia and which is also radicicolous and is placed in the same section of *Collybia* so that it cannot be separated generically at present, appears related to *Lentinus* (15), which is an utterly different stock of agarics!

C. Henriettae may be the same as the Malayan form of *C. radicata*. It is said to have a dry "somewhat downy" pileus (22); otherwise it is indistinguishable. Its rarity in England is understandable if it is the sporadic introduction of a tropical variety.

C. longipes is also close to *C. radicata*, again with the same habitat, the same build of fruit body and similar spores. But the pileus and the stem are dry, though they are evidently provided with palisades, a specific feature of which is the development of stiff brown hairs giving the macroscopic velvetiness. The spores are as variable: Ricken gives them as 9–10 × 6–7 μ (24); Rea as globose, 12–15 μ, and 10–11 μ in var. *badia* Lucand (22); and Bresadola as globose, 9–10 μ, and 13–15 × 11–14 μ in some Chinese specimens. The presence and nature of the cystidia are doubtful, since Ricken alone ventures "very sparse, subulate-cylindric, 50–60 × 8–10 μ," which recalls those of *C. radicata* var. *gracilis* Lange.

I have not had access to a description of *C. cheimonophylla*. But, as Boursier states that *C. alphitophylla* is only a variety of it(3) and as Patouillard's description of *C. alphitophylla*, quoted by Petch(19), is fully covered by that of *C. apalosarca*, *C. cheimonophylla* must be very close if not identical with *C. apalosarca*: on closer inspection, however, it may prove the second hypothetical.

Thus, in summary, there is a group of closely allied species in which the fruit body is gymnocarpic or angiocarpic and varies in size from very small (pileus 4 mm., stem 3 × 1 mm.) to large (pileus 15 cm. stem 20 × 1·5 cm.); in which the pileus is dry or viscid, with one palisade or two palisades and included jelly; in which the stem is perstipitate or discoid below and supra-stipitate, and dry or viscid; in which the gills are decurrent, adnate, sinuate, adnexed or nearly free; in which the spores vary between 9 × 6 μ and 23 × 22 μ; in which the cystidia are sparse or very abundant, and vary in shape from subcylindric to clavate or ventricose and in size from 50 × 8 μ to 280 × 40 μ; in which the habit is solitary or tufted, radicicolous and terrestrial, (perhaps even humicolous), or lignicolous and high up on tree trunks, and extreme temperate or extreme tropical. The members of the group agree evidently in having fruit bodies of Buller's *Armillaria* sub-type, in having a palisade on the pileus and the stem, a fuscous umber pigment in the cell sap, at least of the pileocystidia, smooth white spores and thin-walled cystidia: probably it will be found that the spores and basidia are multiguttulate, and that the gill edge is sterile with a palisade of cheilocystidia. These properties are hardly distinctive.

The genus *Mucidula*

It will be seen how unsatisfactory is the genus *Mucidula*. Some such unit is certainly required, but in our ignorance of the microscopic structure of toadstools how can it be defined? Thus I have preferred the Friesian form genera, though they are so artificial.

Patouillard made the genus to separate *Armillaria mucida* and *Collybia cheimonophylla* from *Armillaria* proper on the basis of the mucilaginous veil and the large spores. In view of the close relation between the species which have just been mentioned in the preceding section, these characters can no longer stand. Once the status of *Collybia apalosarca* is realised, *C. radicata* cannot be separated generically from *Armillaria mucida* in a natural system and *Collybia radicata* has no veil, a dry pileus in some cases and quite small spores in others. Nor can *C. longipes* or *C. atrialba* be separated generically, though still more unlike *Armillaria mucida*.

As emended by Boursier(3), the genus covers *A. mucida*, *Collybia cheimonophylla*, and *C. radicata* in a section "Viscidae" and *C. longipes* in a section "Pilosae." The generic characters are the large globose

spores, the large prominent basidia and cystidia, and the palisade of pileocystidia. The colour of the spores, the formation of the veil and the attachment of the gills are not mentioned, nor is an explanation given of "large" as applied to spores and cystidia, and it is not obvious from the range of sizes which I have just enumerated. *C. radicata* is placed in one section and *C. longipes* in another because the pileocystidia of *C. radicata* are mucilaginous. In this respect the Malayan form of *C. radicata* agrees with *C. longipes* and the sectional distinction fails: presumably, that is, for it is not explained. It is likely that *Armillaria mucida* and *Collybia apalosarca* differ more from *C. radicata* in the superficial structure of the pileus than *C. radicata* does from *C. longipes*.

But it is idle to multiply the genera. Before one can reclassify agarics on the sure lines of a natural system a thorough microscopic morphology must be instated; thorough research is first needed. To show how little is our knowledge of these organisms, one cannot point to a single exclusive property covering the members of this group, yet a natural genus is essentially exclusive, the species linking with other types of organism being extinct. One must search for the co-ordinate species with the brown colour, a sterile edge to the gill and the characters of the first hypothetical in *Collybia* and *Tricholoma*. Then may one look back in *Clitocybe* and *Hygrophorus* for the primitive members and forwards into *Pleurotus* for the most advanced, because it is natural to lignicolous Basidiomycetes with a mesopodal fruit body that they should evolve species with pleuropodal, apodal, sessile and resupinate forms. How do those with an upper gelatinous layer to the pileus and brown colouring, as *Pleurotus mastrucatus* Fr., *P. algidus* Fr., or *P. cyphellaeformis* Berk. or even *P. palmatus* (Bull.) Quél., compare? The field of research is unbounded.

The marginal veil

Concerning the nature of the veil there are two schools of thought. The older, which dates from de Bary (2), has been discredited. It was based chiefly on Brefeld's most detailed observations on *Coprinus* and Hartig's on *Armillaria mellea*. They said that the primordium of the fruit body was gymnocarpic, that the naked rudiment of the pileus was separated from the stem by a slight groove (formed by the annular outgrowth of the limb from the apex of the primordial shaft), and that hyphae grew out from the margin of the pileus and the surface of the stem and met and wove together to form the marginal veil across the groove, which, thus closed, became the gill cavity. To the contrary, the later school of Atkinson and the American mycologists (1, 11) has shown that in many species of *Psalliota*, *Hypholoma*, *Stropharia*, *Pholiota*, *Cortinarius*, *Inocybe*, *Tubaria*, *Lepiota* and in *Armil-*

laria mellea itself the fruit body (comprising stem, pileus and gills) is laid down inside a primordium composed of "interwoven hyphae," and that the gill cavity arises as an annular split among the interwoven hyphae between the developing limb and the primordial stem and does not open to the exterior until the veil is ruptured on expansion of the fruit body. This original tissue of interwoven hyphae is called the ground tissue; that on the outside of the pileus and stem, covering the fruit body, is called the blematogen because it forms the universal veil, and that which persists between the margin of pileus and the stem forms the marginal veil, which is therefore not a later development subsequent to the pileus and stem.

My observations on *Collybia apalosarca* show that, so far from being antagonistic, the two schools of thought are complementary and each is based really on a partial view of the general developmental processes of the agaric fruit body. If it is borne in mind both that the pileus may be exogenous or endogenous and that the hyphae may grow from the margin of the pileus and the surface of the stem, reconcilement is easy. The two processes may be combined in different ways, and as there is abundant evidence for both, a brief description will explain. I have endeavoured also to present the idea visibly in Fig. 13.

Consider first the origin of the pileus. In the least specialised gymnocarpic agarics, such as *Craterellus* and *Cantharellus*, the pileus is exogenous. That is to say, the limb is formed essentially in the same way as I have described in *Polystictus xanthopus* (8), merely by displacement of the main growing region of the primordial shaft from the centre of the apex to the periphery; the peripheral hyphae at the apex of the shaft become the main hyphae of the marginal growing region of the pileus; but owing to epinasty, which is very marked in all agarics, the margin of the pileus tends to grow round towards the stem. But in the first step towards the angiocarpic type, it is not the ends of the main hyphae of the primordial shaft which form the limb but laterals from them: the limb thus arises a short distance below the apex of the shaft. Therefore here and probably in *Clitocybe*, *Hygrophorus* or *Collybia* including *C. radicata*, the pileus may be said to be slightly endogenous, though development in the main is still gymnocarpic (the gill cavity being open from the first), and there is no veil unless one can regard the free ends of the main hyphae of the primordial shaft over the centre of the pileus as the rudiment of the blematogen: such, too, may be the nature of the umbo in *Androsaceus*. In the next step, the hemiangiocarpic, occurring in *Laccaria laccata* (11) and *Collybia apalosarca*, the laterals forming the limb arise still more internally so that the layer of free hyphal ends over the primordial pileus is more conspicuous and is continuous with the palisade on the primordial shaft. There is, in fact, in this case a rudimentary blematogen,

Fig. 13. A scheme showing the different methods of making the veils in agarics: *a*, the primordial shaft, corticated and with the medullary hyphae beginning to enlarge; *b* and *g*, developing a pileus exogenously; *c* and *h*, developing a pileus slightly endogenously; *d* and *k*, developing a pileus deeply endogenously; *e*, a gymnocarpic primordium with outgrowth from the surface of the stem; *f*, a gymnocarpic primordium with outgrowth from the margin of the pileus; *l*, a gymnocarpic primordium with outgrowth from the surface of the stem and the margin of the pileus.

because the palisade over the primordial stem and pileus grows for some while after the limb is started and it forms a thin universal veil which prevents the primordial limb from breaking through to the exterior: the gill cavity arises internally as a gap between the limb and the stem. Then lastly in the angiocarpic type, the laterals which form the limb arise very deeply at such a distance below the apex of the primordial shaft that a very thick layer remains distal to the pileus and forms the easily recognisable blematogen: the pileus is deeply endogenous and the gill cavity is closed from the first.

Consider then the second process. Hyphae may grow out from the surface of the stem and the margin of the pileus whether the pileus is exogenous or endogenous in any degree. Among gymnocarpic species there is a slight outgrowth from the margin of the pileus in *Clitocybe cerussata* which is more marked in *Clitopilus noveboracensis*(11), and it is most striking in the section of *Lactarius* including *L. torminosus*. Outgrowths from the stem are exceedingly common, for example the palisade in *Collybia radicata* or the shaggy villousness of *Paxillus atrotomentosus*. In *Pluteus admirabilis* one has an example of outgrowth from the pileus in a species in which the limb is probably slightly endogenous: hyphae grow from the incurved margin of the primordial limb and interweave loosely with hyphae on the stem but insufficiently to form a marginal veil(11). This case leads to the similar condition in the hemiangiocarpic type shown by *Collybia apalosarca*: the very rudimentary blematogen is reinforced by outgrowths from the pileus and the stem, but again insufficiently to form a ring. This in turn leads to the angiocarpic species. In *Tubaria furfuracea* and *Armillaria mucida* the pileus is fairly deeply endogenous and in *Psalliota* it is very deeply endogenous, yet such marginal outgrowth from the pileus occurs abundantly in these species(11): in *Pholiota squarrosa* and *P. flammans* it is particularly extensive(11). Then in *Coprinus ephemerus*, *C. ephemeroides*, *C. lagopus*, and *C. stercorarius*, according to Brefeld, one has the rare combination of an exogenous pileus with subsequent angiocarpic development through such secondary outgrowths which are mainly from the base of the stem. And I see no reason to doubt, as Atkinson does, his observations on the ground of poor technique; for, it may be remarked in this connection, that a great deal more can be learnt about the development of fruit bodies from hand sections of fresh material than from microtome sections: the sections must be thick in order to trace the course and branching of the hyphae, and while fairly thick sections of fresh material are still beautifully transparent, thick microtome sections are opaque and in thin ones the hyphae are chipped into bits and cannot be followed through the tissue.

The presence of a universal veil depends primarily on whether the pileus is exogenous or endogenous: the presence of a marginal veil

depends more particularly on the outgrowths from the margin of the pileus and the stem. If the amount of both blematogen and marginal growth is small, there will be a cortina of varying thickness, *e.g. Tricholoma* and *Cortinarius*; if the blematogen is practically absent and marginal growth slight, the veil will be as rudimentary as in *Pluteus admirabilis* or *Collybia apalosarca*. If the amount of both is great, then the universal veil forms scales on the pileus and the infra-annular portion of the stem and the marginal veil forms the inferior annulus, *e.g. Armillaria* and *Pholiota*; if the marginal veil separates from the stem as well as from the pileus it forms the movable ring, *e.g.* the supra-stipitate species of *Lepiota* as *L. procera*. If the amount of blematogen is small and the marginal outgrowth of the pileus relatively great, the marginal veil is torn from the stem and is appendiculate from the edge of the pileus, *e.g. Hypholoma appendiculatum* (and perhaps *Panaeolus sphinctrinus* etc.). If the blematogen is very well developed, coherent and separated from the pileus by a cleavage layer of loose aerenchymatous or gelatinous tissue, the universal veil forms the volva as the pileus slips out of it, *e.g. Amanitopsis* and *Volvaria*.

There is the final complication in the *partial veil*. It is formed from hyphae which have grown from the surface of the stem into the gill cavity, and it is really only an elaboration of the palisade on the supra-annular portion of the stem as the proximal part of the universal veil is an elaboration of that on the infra-annular portion. In its most highly developed state in *Amanita* and *Psalliota*, the palisade forms a thick coherent tissue firmly connected with that of the marginal veil, which is also well developed. On expansion of the primordium both the marginal veil and the partial veil are peeled off the stem from below upwards and stretched as a membrane under the gills, but when the pileus is half-expanded the partial veil is torn from the marginal veil and drops back on to the stem as a loose sheath pendant from the apex and known as the superior annulus: the marginal veil is thus appendiculate in fragments from the pileus. Nevertheless one can perceive in *Collybia apalosarca* the rudimentary homologue of the partial veil in the palisade on the supra-annular portion of the stem, as well as the homologue of the blematogen in the loose cortex of the primordial shaft, and the homologue of the marginal veil in the anastomosis between the margins of the limb and disc. In *Amanita* these slight outgrowths have become thick, recognisable layers and ornaments to the umbrella.

The difficulties met with in comparing the development of the fruit body in agarics are mainly difficulties of description. One cannot delimit exactly the parts; the stem merges into the pileus and the pileus into the gills; the surface of the pileus merges into the universal veil and this into the marginal veil which merges into the partial veil; even the hymenium may be ill-defined as it often occurs

on the stem for some distance below the gills. But in studying the development one must determine the sequence of the hyphae in their manner of apical growth and branching in the primordium, before the interrelations of the parts can be understood. In mature fruit bodies, whether gymnocarpic or angiocarpic, the hyphae in the stem, limb and gills are nearly always longitudinal with respect to the parts (though a curious exception may occur in *Gyroporus castaneus* in which the main hyphae in the stem appear transverse or tangential!), and the hyphae of the stem are joined as laterals to those of the mycelium, the hyphae of the limb as laterals to those of the stem apex, and the hyphae of the gill trama as laterals to those of the limb. The sequence implies acropetal development of the whole fruit body with apical growth of the parts and subterminal branching originating each part successively: the base of the stem must be formed first, then the shank of the stem, then the limb, and lastly the gills. One cannot imagine how else the parts may develop when there is this connection between their hyphae, yet several investigators affirm that it is by no means always so. It is said that the hymenophore is "differentiated" first in *Armillaria*, *Psalliota* and *Stropharia*, and that the pileus is "differentiated" first in *Hypholoma*, *Tubaria*, *Amanitopsis* and *Amanita*, so the parts must then float into existence independently in the primordium and subsequently become joined together, rather in the way that the Cheshire cat came upon Alice in Wonderland. But, of course, all primordia are initiated as a primordial shaft, the body of which becomes the stem, and the stem is therefore always the first part to be defined. Nor is it clear how the inception of the parts is recognised, as it is stated, from their "differentiation": there is no differentiation of the hyphae according to the parts, the fruit bodies being monomitic, and the differences in staining power of the hyphae, which are shown in the explanatory microphotographs, are caused by the vacuolation of the cells and alterations of the hyphal walls, and such processes succeed inception of the parts. I am inclined to turn the tables and champion Brefeldian technique against Atkinson's: though there are many papers on the subject(13), I doubt if anyone could describe even how the common mushroom is formed inside a body of interwoven hyphae by the apical growth and branching of another set of hyphae. But when development is explained as the consequence of the properties of hyphae in an organic whole, such notions may also fade into a smile.

Morphological remarks

Collybia apalosarca shows well a common factor in the equipment of multifilamentous plants, whether algal or fungal. It is the formation of a level at the surface or boundary of a tissue by sympodial branching. The factor becomes particularly important in agarics through the

development of the palisades and their elaboration into the veils. In both alga and fungus the level results from the manner of growth of the soma. Apical growth is retarded in the filaments at the periphery of the growing point and their free ends are splayed aside by the laterals which continually arise in the centre of the growing point. As they accumulate, therefore, the free ends of the peripheral filaments are perforce rotated through more or less of a right angle and come to point outwards perpendicularly to the long axis of the soma. A longitudinal section of such a growing point reveals the fountain effect of Oltmanns—his "springbrunnen-typus" (18). But here comes the difference. In both algae and fungi the medullary filaments, composed of the fixed proximal parts of the filaments, begin to enlarge and without some compensatory process the free cortical filaments would be pulled apart to form a sparse pile of hairs. In algae the free ends of the filaments continue to grow out, branching repeatedly, and they form the compact, small-celled, photosynthetic cortex, the increase in surface of which may exceed that allowed by the enlargement of the medulla and so the medullary filaments may be pulled apart to form mucilage spaces or air cavities. In fungi, on the contrary, the outgrowth of the free ends is soon arrested: laterals then arise from the subterminal cells and, on reaching the level of the terminal cells of the parent filaments, they stop growing and branch sympodially in their turn: a palisade of greater or less density is thus constructed. In fungi, moreover, the cells of the palisade, not being photosynthetic or absorptive, generally enlarge also. In the simplest cases, as in *C. apalosarca*, only the terminal cells enlarge but in many others, in the palisade on the stem of *C. radicata* or in the cortex of the apothecium in Discomycetes, for example, one or more of the subterminal cells enlarge and a compact pseudoparenchymatous layer is constructed. In few fungi, however, is the intercalary growth of the sterile palisades sufficient to prevent disruption on expansion of the primordium: in most, the palisades are broken up into squamules or scurfy or pruinose particles. But the hymenium is never disrupted because such enormous numbers of basidia are intercalated: it often happens, instead, that the hymenium disrupts the medulla, as in *Physalacria*, *Pistillina* and many other Clavariae and the Clavuleae.

The branching and inflation of the cells of the palisades in fungi also enables one to recognise a characteristic plectenchymatous underlying layer or *hypoderm* of which the subhymenium is merely a special case. The hypoderm comprises the proximal parts of the hyphae of the palisade and they are always closely interwoven or interlocked because the laterals in finding their way to the surface push between the pre-existing hyphae and often arrive at some distance from their parent hyphae. Then, on inflation, their cells are pulled this way and that and often become looped and stretched and still more entangled

with each other. Thus the hypoderm, including the subhymenium, always develops after the palisade, including the hymenium, has been defined.

The time-factor must enter into comparisons not only of the size and degree of development of parts but even of the shape of the individual cells. Dimorphism between cheilocystidia and pleurocystidia occurs in many genera which are not nearly related, as in *Inocybe*, *Pluteus*, *Psathyra* and *Mycena*, and it may generally be a matter of unequal development through the late inception of the cheilocystidia, just as in *C. apalosarca*. The large ventricoso-fusoid pleurocystidia, and pileocystidia, must pass through a clavate stage during the inflation of the cylindric terminal cell and their final shape is reached through the protrusion of the apical part. If growth is arrested before development is completed, the cystidium will have an unfinished appearance. Thus, in cases of dimorphism, the cheilocystidia are mostly clavate and of simpler structure than the pleurocystidia and there are transitions on either side of the gill edge, *e.g. Inocybe*, or *Pluteus*, with thick-walled ventricoso-fusoid pleurocystidia and thin-walled clavate cheilocystidia. As the pileocystidia of *C. apalosarca* pass through a clavate stage, so may one expect the less advanced species in the group to have clavate pileocystidia, *e.g. C. radicata*. The caulocystidia of *C. apalosarca* are also clavate because they are among the last terminal cells to be inflated. It will be interesting to learn the nature of the hairs of *C. longipes*; for this species is gymnocarpic and the normal acropetal development of the palisades should be less transposed and large caulocystidia would be expected.

The non-inflation of the cells of the hyphae forming the internal palisade of the pileus in *C. apalosarca* illustrates another common feature in the histology of fungi. In a gelatinous tissue, in which the walls of the hyphae are mucified, the constituent cells are rarely inflated. It seems that the mucilage absorbs the water which is normally available for the inflation of the cells, or that some alteration of the plasma membrane, following mucification of the wall, prevents the cells from developing their normal osmotic system.

Summary

The structure and development of the fruit body of *Collybia apalosarca* B. & Br. is described in detail as a multifilamentous soma formed by the apical growth and ramification of hyphae with modification of the cells on cessation of growth.

A specific description is given, based on Malayan material, and a new variety *perstipitata* and a new form *radicans* are proposed.

In the mature fruit body all external and internal surfaces between tissues are bounded by palisades of free hyphal ends the terminal cells

of which have characteristic shapes. On the pileus there is a thick gelatinous layer derived from the blematogen and bounded by an external and an internal palisade.

Development is indirect and hemiangiocarpic. A short, loosely corticated primordial shaft is first formed. At the apex of the shaft the limb arises slightly endogenously. There is a rudimentary blematogen with a rudimentary marginal veil reinforced by the outgrowth and anastomosis of hyphae from the margin of the pileus and the surface of the stem, but there is no ring or cortina. The gill cavity is more or less closed at first. Development is strictly acropetal with apical growth of the parts of the fruit body followed by intercalary growth at the surfaces by sympodial branching, which multiplies the tissue-elements and compacts the palisades, and finally with inflation of the medullary hyphae causing expansion of the primordium. The base of the primordial shaft becomes the base of the stem; the body of the shaft becomes the shank of the stem; the apex becomes the centre of the pileus while the limb is formed by marginal growth from the apex of the shaft and the gills by marginal growth in centrifugal lines on the proximal side of the limb. Inflation of the hyphae proceeds acropetally from the base of the stem and reaches a maximum in the supra-annular portion of the stem and the central portion of the limb on the night of expansion. In the typical form the infra-annular portion of the stem is enlarged into a supporting disc which does not elongate; in var. *perstipitata* the stem elongates throughout and there is no disc.

Biologically, the fruit bodies belong to Buller's *Armillaria* subtype.

By correlating in different fruit bodies the average elongation of the cells in the mature stem with the length of the mature stem, it is shown that the great variations in size of the fruit body (from 3 mm. to 9 cm. high) are due either to juvenescence or to differences in the inflation of the cells.

The arrangement and number of the gills are also correlated with the size of the fruit body. Those with a thick stem apex generally have more primaries than those with a thin stem apex, and those with a wide limb more ranks than those with a narrow limb, from which conclusion additional proof is given that small fruit bodies are generally juvenescent.

C. apalosarca is intermediate in many respects between *C. radicata* and *Armillaria mucida*. The three species are compared as fully as possible. The structure of the mature fruit body of *Collybia radicata*, as it occurs in Malaya, is described and the relevant facts about *Armillaria mucida* are summarised.

In all three species the construction of the fruit body is essentially the same. But *Collybia radicata* has a single palisade on the pileus,

without a gelatinous layer, and is evidently gymnocarpic. *Armillaria mucida* has evidently the same structure of the pileus as *Collybia apalosarca* but is angiocarpic with an inferior annulus. These and other minor differences are evaluated by certain general propositions concerning the evolution of agarics. The three species are considered specialised offshoots of two hypothetical ancestral species: while the first hypothetical is probably extinct, the second may be found in tropical America or the south temperate zone.

The morphology of the marginal veil is reconsidered. The investigation of *C. apalosarca* shows that there is really no antagonism between de Bary's early account and that of the modern American school, since each is based on a common developmental process in agarics and is partly correct. The formation of the marginal veil may depend on the outgrowth and anastomosis of hyphae from the margin of the pileus and the surface of the stem, as de Bary held, as well as on the presence of a blematogen, as the American school maintains: both factors may be equally important, or the one or the other ascendant. It is shown further how the presence of the blematogen depends on the endogenous origin of the limb and how the marginal veil is related to the universal and partial veils.

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PHYTOPHTHORA MEGASPERMA DRESCHLER IN TASMANIA

By W. J. DOWSON, M.A., D.Sc.

Lecturer in Mycology, Cambridge University; late Plant Pathologist, Department of Agriculture, Tasmania

In the Tasmanian autumn, *i.e.* April–May, of 1931, many complaints were received by the Department of Agriculture of Tasmania from Sydney, New South Wales, relating to the bad condition of carrots exported from the north-west coast of the island State.

Carrots have been grown for export for some years in the reclaimed swamps round the town of Smithton where heavy yields are obtained. The crop is dug, bagged immediately and sent by lorry or train to the port of Stanley to await shipment to the mainland, either direct to Sydney or by a longer route along the north-west coast of Tasmania and thence to Sydney. The sea journey occupies from two to four days according to the route taken, and the carrots remain enclosed in the bags for about a week.

The autumn of 1931 was abnormally wet so that the crop was dug, bagged and transported to Sydney under exceptionally humid conditions. A sample of a consignment returned from New South Wales was in such a rotten condition as to render diagnosis of the possible cause impossible; but the most striking symptom was a black discoloration of the tissues. The Port Inspector at Stanley was warned to look out for dark soft marks, during his inspection of carrots for export. This resulted in a sample being sent to the laboratory at Launceston with the information that the contents were probably what the Sydney inspectors were complaining of. At about the same time a further sample was returned to Tasmania from Sydney in not quite such a bad state; on comparing the two samples the rotting seemed to be similar.

The lowermost part of the roots, often including the very apices, was soft and black. Various fungi including *Rhizoctonia* (*Corticium*) *Solani* were observed in the surface layers of the cortex of such diseased areas, but the blackening did not extend beyond these and the rotted interior was never discoloured, only "water-soaked" in appearance.

Microscopical examination of the softened tissue, particularly at the edge next to sound areas, revealed a fairly abundant intercellular mycelium composed of relatively stout aseptate hyphae. Further examination showed that in the blackened layers of the cortex exceedingly numerous spherical, thick-walled resting spores were present, recalling in appearance the oospores of a Phycomycete.

No difficulty was encountered in isolating the aseptate mycelium which grew slowly on potato agar with a rather diffuse growth. Better growth resulted in hanging drop cultures of potato agar, possibly because these were more humid than plate cultures. Luxuriant growth took place on steamed plugs of carrot and potato. Oogonia and antheridia, mostly of the amphigynous type, were produced on the above media but all attempts to induce the formation of sporangia were unsuccessful.

Further subcultures were made in England on other media such as potato-glucose agar, oat-meal agar and corn-meal agar; on all there was a luxuriant growth with the production of sexual organs but no sporangia. When pieces of mycelium from plates of any of the above media were placed on slices of young, fresh carrots, kept moist in deep Petri dishes at a temperature of 25° C., a slow rot developed in the course of some weeks similar in appearance to that observed in the original carrots. No infection was observed through the unwounded surface and none was obtained when portions of mature carrots were inoculated.

At this point cultures were sent to the Imperial Mycological Institute where the *Phytophthora* was identified as *P. megasperma* Dreschler (*Rev. Appl. Mycol.* II, 302) and, following the advice of Mr S. F. Ashby, sporangia were eventually obtained in water cultures a fortnight old.

Information from Tasmania showed that no complaints had been received from New South Wales during the season 1931–2 which was very much drier than the previous season: it would seem that the abnormally wet conditions were primarily responsible for altering the general equilibrium between carrots and soil-dwelling fungi in favour of the latter. Under such conditions infection probably took place, and there is no doubt that once infected the invasion of the tissues developed rapidly during transit, more particularly in the steamers' holds.

NAUMOVIA ABUNDANS DOBROZR.

By J. RAMSBOTTOM

(With Plate I)

In 1926 the late Mr D. A. Boyd sent me a specimen of a Pyrenomycete growing on *Prunella vulgaris* which had been gathered by Miss M. L. Miles at Caputh, Perthshire in Sept. 1912. I was unable to find spores and could make no guess at its identity: this I believe was also the experience of other mycologists to whom specimens were sent. The following year, after the Aviemore foray, I found the fungus on a wayside bank just above Pitlochry. Again I was unable to find spores.

Shortly afterwards a description of the fungus by Dobrozrakova appeared in *Morbi Plantarum*, XVI (1927), 197–9, with the name *Naumovia abundans*. It had been first observed by N. A. Naumov in the Luga district of Russia but in an immature state. Dobrozrakova gathered it from a rather wide area in July, 1926, and, in order to obtain ripe asci, she marked some plots containing infected plants and transplanted others; the fungus was found fully mature in both series the following May and June.

Naumovia was gathered in abundance at the Belfast Foray (1930) and I found it later at Monaghan though it had not been noticed in three weeks' general collecting farther south. It has also been gathered in several districts in England, *e.g.* Newcastle, Leicester, Haslemere.

I made two attempts to transplant infected plants to my garden but, probably on account of delay, without success. I therefore asked my colleague Mr George Taylor to look for old infected stems when botanizing in Scotland and he succeeded in obtaining mature fruits at Reston, Berwick, in April, 1933 (Pl. I, figs. 3 and 4).

Infection may occur when the host plant has only two or three leaves. All vegetative parts of the plant are affected except the roots and the flowers though the stalk of the inflorescence is often crowded with perithecia. The general appearance of the fruit bodies is shown in Pl. I, fig. 1. According to Dobrozrakova "strongly infected plants look depressed, do not flower, or the inflorescence is shortened and the flowers fall off prematurely." On the whole one may say that the fungus develops most markedly in moist places though it is to be found in dry habitats. The original diagnoses are as follows:

Naumovia. Stromatibus firmis, carnoso-lignosis, bene evolutis et delimitatis, longitudinaliter confluentibus, subepidermicis, dein liberis, atrofuscis, parenchymaticis. Peritheciis superficialibus, papil-

lato ostiolatis. Ascis cylindraceis, aparaphysatis; sporidiis filiformibus septatis subhyalinis.

N. abundans. Peritheciis stroma insidentibus, 10–20 et multis longitudiner, aggregatis, sphaericis, 225–350 μ diam., epidermide primo tectis, dein rima longitudinali prorumpentibus et definitive liberis. Stroma ac parietibus perithecii parenchymaticis. Ascis cylindraceis, breve pedicellatis, chlorinis, 67–97 μ long., 4·5–7·5 μ cr., basi coalitis. Sporidiis biseriatis, filiformibus, utrinque acutiusculis, rectis v. sepius curvulis, multiguttulatis, dein multiseptatis (1–6), 30–39·5 μ long., 1·5–3 μ cr., subhyalinis.

Hab. in planta tota: caulibus, stolonis, foliis et inflorescentiis vivis *Brunellae vulgaris* parasitice.

Dobrozrakova places it in Cucurbitariaceae near to *Gibberidea*.

The British specimens agree perfectly with this description, measurements of the Reston specimens being, perithecia 250–350 μ diam., asci 60–100 × 4–7 μ, spores, slightly curved, 38 × 2 μ (average).

The records of *Naumovia* in Great Britain suggest that it first became common in Scotland and that it spread thence to the southern counties of England.

Dobrozrakova says "it is difficult to understand why this parasite has not been noticed before, since its effects are very characteristic." In my experience heavily infected plants tend to have an etiolated appearance often being elongated and somewhat yellowish.

It would be remarkable if Miss Miles and N. A. Naumov should stumble across such a well-marked and characteristic fungus as they did if it had always been as common as it is now. When I found it at Pitlochry I was hurrying along in a very heavy thunderstorm and merely stopped to gather some plants which were obviously diseased; I saw that a fungus was present but I could not then see what it was. It is only comparatively recently that mycologists generally have begun to look for the fungus: previously it was the diseased *Prunella* that was gathered and the fungus thus found. Those who first saw *Naumovia* at the Belfast foray will recollect that this was their experience.

This being so it is inconceivable that the fungus should have been overlooked until recently and then be constantly found independently by different mycologists who were unaware of its identity.

Is the fungus a recent introduction to this country? It is always unsafe to suggest such a hypothesis when the host plant is uncultivated. If it is a recent introduction whence did it arrive? A sudden appearance of a fungus is always a matter of interest from the standpoint of distribution and there are many records of such phenomena in our own literature. The present example differs from these, however, in that the fungus is not one known previously elsewhere, and being introduced to new conditions becomes epidemic usually to become

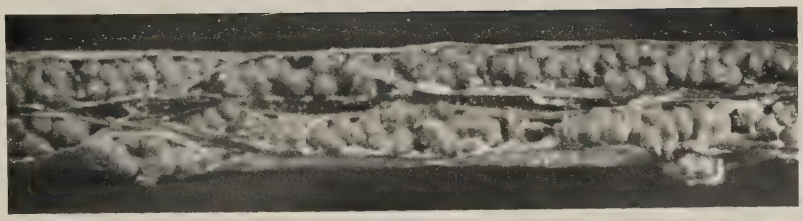

Fig 1

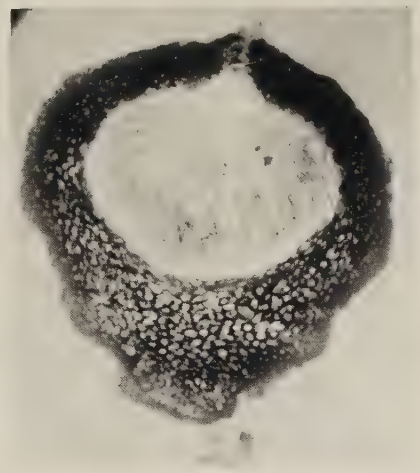

Fig. 3

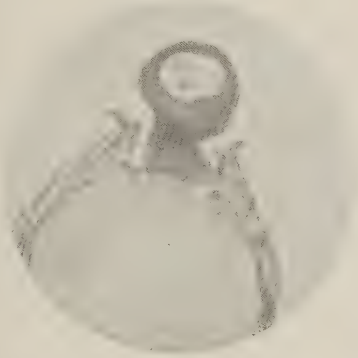

Fig. 2

Fig. 4

Naumovia abundans Dobrozr.

much less rampant later. So far as I have been able to find out *Naumovia* has not been lurking under another name—it is an entirely newly described fungus.

We speak loosely of "new species" and "new genera" sometimes as if they were really new creations and not merely descriptions or diagnoses. Here there might be a temptation to consider the fungus as an entirely new entity and to offer suggestions about how it might have originated. It would certainly be an interesting phylogenetic exercise to tax one's ingenuity in suggesting the possible evolution of so characteristic a Pyrenomycete but it would entail nothing but sterile speculation. All that we can say with certainty is that *Naumovia abundans* was first noticed in Scotland in 1912 and in Russia in 1926 and that it is now widespread in the British Isles, often occurring in considerable quantity.

I wish to thank Miss F. L. Stephens for help in section-cutting, Mr E. H. Ellis for the photomicrographs and Dr B. P. Uvarov for translating Dobrozrakova's paper.

EXPLANATION OF PLATE I

Fig. 1. Infected stem of *Prunella*. The infection was heavy from the tip of the inflorescence to the rootstock (× 11).
Fig. 2. Section of perithecium and host (× 20).
Fig. 3. Section of mature perithecium (× 144).
Fig. 4. Asci and spores (× 1100).

PROCEEDINGS

Meeting held at University College, London, Jan. 20th, 1934, Dr B. Barnes, President, in the Chair.

A. H. Reginald Buller. *Omphalia flavida*, a Luminous and Gemmiferous Leaf-spot Fungus.

Omphalia flavida, the cause of the American coffee-leaf disease, is a luminous and gemmiferous leaf-spot fungus. It attacks not only coffee leaves, but also the leaves of a great many different hosts included in the Dicotyledons, Monocotyledons, and Ferns.

In pure cultures, as Ashby first observed, the mycelium produces in succession: (1) *gemmifers*, hitherto misnamed "*Stilbum-bodies*," and (2) perfect agaricaceous *sporophores*.

Each gemmifer is yellow and consists of a slender solid tapering *pedicel* about 2 mm. long and of a terminal, detachable, multicellular *gemma*, shaped like the knob of a door-handle and about 0·36 mm. in diameter. The structure of a gemmifer has been redescribed in detail. The gemma is regarded as a reduced, gillless, sporeless, detachable pileus. A gemma, after being blown by the wind on to a leaf, sends out hyphae which penetrate the epidermis and produce a leaf-spot. On the leaf-spot about thirty to fifty new gemmifers are soon developed. The leaf-spots on coffee leaves owe their origin to gemmae which seem to have largely taken the place of basidiospores as a means of propagating the species.

The mycelium and gemmae of *Omphalia flavida*, both in artificial cultures and in leaf-spots, are luminous. This discovery has provided a means for diagnosing the American coffee-leaf disease in the dark. At night, in a Porto Rican coffee plantation, Professor Albert Müller was able to see coffee leaf-spots very clearly at a distance of 2–3 ft. from the leaves and less clearly, although distinctly, at a distance of 6–10 ft.

Kathleen Sampson. The Presence and Absence of an Endophytic Fungus in *Lolium temulentum* and *L. perenne*.

A critical survey of the literature indicates that it is incorrect to assume, as certain writers do, the identity of the seed fungus of *Lolium* and the organism, apparently a Phycomycete, which occurs in the roots.

The following observations refer to the first fungus, an intercellular endophyte of uncertain affinity which invades the vegetative organs and the seed.

Single plants of *L. temulentum* selected in 1929 formed the starting-point for pure lines which have been studied during four seasons. The presence or absence of the fungus was determined by an examination of pith scraped from a flowering stem and stained with cotton blue. Ovaries and seeds which were sectioned confirmed the results obtained by this method.

Lines classified on this basis remained true to type for four generations. When reciprocal crosses were made, the hybrid was infected only if the female parent carried the fungus. This made it possible to compare plants of similar genetical constitution which differed only in the presence and absence of the fungus. Two series of F_1 plants produced by reciprocal crossing and examined in regard to growth, yield and chemical composition, gave no indication of either a stimulating or a depressing effect resulting from invasion by the endophyte.

Free and infected races of *L. perenne* were also studied and transmission by the female parent was found in suitable crosses.

The fungus, which is present in tiller buds and leaves, was distributed by vegetative propagation of infected plants.

N. J. G. Smith and F. B. Pope. The Association between the Gasteromycete *Polysaccum* and *Eucalyptus* Roots.

In the Eastern Cape *Polysaccum crassipes* seems invariably to occur under *Eucalyptus* trees, although in the Western Cape we have seen it under *Leptospermum* and Bruns* found it under pines in Europe.

The hot sandy soil of the Cape frequently contains rhizomorphs of no other fungi. *Polysaccum* mycelium, moreover, is usually yellow and is easily traced. Its mode of life is various: a saprophytic life in the soil is followed by some hyphae, others live on or among the bark layers of living roots, as noted by Van der Bijl†; sometimes the fungus is parasitic or it may form mycorrhiza. That both of these last-named relations can exist in different branches of the same root is most interesting.

The parasitic condition involves a free spread of inter- and intracellular hyphae, accompanied by the death of root cells. The invasion is not confined to the outer cells but penetrates deep into the xylem. Parasitised roots are thin, but old enough to have a corky covering. Younger roots, that are still in the absorptive stage, become mycorrhizal, and show yellow coralloid clusters of much the same form as Melin's‡ racemose mycorrhiza of spruce.

All the main internal features (the layered fungus mantle, the palisade-like epidermal cells with "Hartig-net" mycelium) are paralleled in Melin's descriptions of other tree mycorrhiza. The fungus is usually present inside the cells of the epidermal layer and the outermost cortical layer but rarely occurs in any deeper layer. Intracellular digestion of hyphae is exhibited with a clarity unusual in tree mycorrhiza.

The fungus grows best on agars made with a decoction of *Eucalyptus* roots but even on these it does not grow very well so that experiments on the inoculation of roots with pure-culture mycelium have not progressed far.

W. H. Wilkins. Preliminary account of the parasitism of *Ustulina vulgaris*.

The amount of rot present in an infested lime and a beech was described and a summary given of the author's introductory paper (*Trans. Brit. Mycol. Soc.* xviii (1934), 320–46).

* Bruns, E., "Beitrag zur Kenntniss der Gattung *Polysaccum*," *Flora*, lxxviii (1894), 67–75.

† Van der Bijl, P. A., "Note on *Polysaccum crassipes* D.C.: a common fungus in *Eucalyptus* plantations round Pretoria," *Trans. Roy. Soc. S. Africa*, vi (1917), 209–14.

‡ Melin, E., "Experimentelle Untersuchungen über die Konstitution und Ökologie der Mykorrhizen von *Pinus silvestris* L. und *Picea Abies* (L.) Karst.," *Falck. Mykol. Unters. und Berichte*, ii (1923), 73–331.

REVIEW

Die Pilze Mitteleuropas. Band I. Die Röhrlinge, by F. KALLENBACH. Lief. xii. Pp. 79–86. Pls. 30, 31. Leipzig, Werner Klinkhardt, 1934.

The previous part of Kallenbach's Monograph was published in 1930 and mycologists had begun to fear that the work would never be completed. The remaining parts are promised at six-monthly intervals. Meanwhile Band II is announced to begin this year and will deal with *Lactarius* (B. Knauth) and the Tremellineae (W. Neuhoff). It is to be hoped that the revised time-table can be kept to for it is eight years since the first part of the *Boletus* monograph appeared. There can be no doubt that it will be the standard work on the genus for many years to come, but most students would have preferred to have a complete though expensive volume now rather than parts in paper covers appearing at odd intervals over such a number of years. We trust that the publisher has most of the material for the next volume in hand before he begins publication.

The present part of the *Boletus* monograph has two coloured plates and eight pages of text.

The first plate shows most excellent representations of the fungus usually called *Boletus erythropus* but to which the name *B. miniatoporus* Secr. is given. Persoon used the specific epithet *erythropus* for the species which is now most frequently called *B. Queletii.* Fries adopted Persoon's name only, first applying it to the fungus figured here, in 1818, giving it specific rank, but reducing it to varietal rank (var. of *B. luridus*) in the *Systema.* The International Rules start from this work and so unfortunately it means that we shall have to take the first specific name after Fries: it looks as if this is *B. perniciosus* Roques.

A key is provided to the species of *Boletus* with reddish orifices to the pores. These species were all figured conveniently on Plate 2: *B. Satanus, B. rhodoxanthus* = *purpureus, B. erythropus* = *Queletii, B. miniatoporus* = *erythropus,* and *B. luridus.* The first essential to a better understanding of the genus is well on its way, i.e. the clear definitions of the species—the precise nomenclature can wait awhile.

The second plate figures *B. appendiculatus.* It is perhaps printed a little too reddish brown as the author states but the fact that he has chosen to comment upon this shows the general excellence of the plates.

J. R.